

Psychology of a Superorganism

by

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## ABSTRACT

For over a century, researchers have been investigating collective cognition, in which a group of individuals together process information and act as a single cognitive unit. However, I still know little about circumstances under which groups achieve better (or worse) decisions than individuals. My dissertation research directly addressed this longstanding question, using the house-hunting ant *Temnothorax rugatulus* as a model system. Here I applied concepts and methods developed in psychology not only to individuals but also to colonies in order to investigate differences of their cognitive abilities. This approach is inspired by the superorganism concept, which sees a tightly integrated insect society as the analog of a single organism. I combined experimental manipulations and models to elucidate the emergent processes of collective cognition. My studies show that groups can achieve superior cognition by sharing the burden of option assessment among members and by integrating information from members using positive feedback. However, the same positive feedback can lock the group into a suboptimal choice in certain circumstances. Although ants are obligately social, my results show that they can be isolated and individually tested on cognitive tasks. In the future, this novel approach will help the field of animal behavior move towards better understanding of collective cognition.

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## Chapter 1

### INTRODUCTION

Psychology is “the study of the mind ”— the perceptual experience that an organism internally has while interacting with the external world (Gazzaniga, Heatherton, and Halpern 2012). One of its main goals is to understand the mechanisms by which organisms acquire, process, and store information from the environment. These mechanisms are collectively known as cognition, which includes perception, learning, and memory (Shettleworth 2009). Psychologists have demonstrated the cognitive abilities of not only humans but also other species, from insects to primates (Dukas 1998; Papini 2008; Pearce 2008; Shettleworth 2009). For example, although the brain of honeybees has only 0.01% as many neurons as that of humans, they demonstrate the ability to complete complex cognitive tasks (Chittka and Thomson 2001; Menzel and Giurfa 2001a).

There are broadly two levels of explanations for cognition. First, the “ultimate explanation” is why existing cognition evolved. It deals with the question “what is the fitness benefit of certain cognition?” Cognitive abilities evolved by means of natural selection and thus should be adaptive in their environment. For example, homing pigeons are well-known for having internal maps with detailed landmarks (Wallraff 2005; Gazzaniga, Heatherton, and Halpern 2012). An ultimate explanation would be that the navigation abilities enable pigeons to acquire information about their position relative to food and mates and thus increase their fitness. Alternatively, “proximate explanation” is a mechanism underlying a

behavior. Proximate causes are usually specified at levels right down to events, such as hormones and neurons (Dukas 1998; Papini 2008; Pearce 2008; Shettleworth 2009). To continue with pigeons as an example, it has been suggested that neural activity in the hippocampal formation is responsible for this navigation ability (Gagliardo, Ioalé, and Bingman 1999).

In this dissertation, I investigated collective cognition, in which a group of individuals that together process information and act as a single cognitive unit (Hofstadter 1999; Couzin 2009; Marshall and Franks 2009). I looked at this phenomenon at both the ultimate and proximate levels of explanation. At the ultimate level, I seek to understand whether collective information-processing increases fitness. Because the group success sometimes affects individual fitness, members may cooperate and coordinate with each other to induce advantageous collective decision-making (Smith 1964; Wilson 1973; Wilson 1975). For example, a colony of cockroaches more likely chooses the better shelter between two than lone individuals (Canonge, Deneubourg, and Sempo 2011), and a flock of pigeons uses more efficient homing routes than an individual (Biro et al. 2006). At the proximate level, studies of collective cognition have shown that it relies on decentralized mechanisms in which members have non-linear responses to information from others and positive feedback brings the group to consensus decisions (Conradt and Roper 2005; Detrain and Deneubourg 2006; Dussutour, Fourcassié, and Jeanson 2012)

As of yet, I have not challenged cognitive groups beyond rudimentary tasks such

as choosing one of two options, and so I still do not know full cognitive capabilities of animal groups. To investigate these, I applied concepts and methods developed in psychology to animal groups. Psychologists have focused on individual human cognition and described it in detail. Because a cohesive animal group acts as a single cognitive unit, I can apply the very same psychology approaches to animal groups to investigate different aspects of collective cognition. In this way, I can analyze cognition at both the ultimate level (e.g. are certain collective cognitive abilities superior to those of individuals?) and the proximate level (e.g. how do individuals collectively achieve these abilities?).

I have used this strategy to investigate collective cognition in social insects. Because of the high genetic relatedness among colony members, individuals gain fitness benefits from the their colony's success, rather than their own (Hölldobler and Wilson, 2008). This has allowed selection to shape extremely unified collective behavior, and thus colonies of social insects can be considered as a superorganism, analogous to a single organism (Hölldobler and Wilson, 2008; Seeley, 1989; Wheeler, 1911). A superorganism offers some of the most compelling and well-studied examples of collective cognition (Franks 1989; Seeley 1997; Hirsh and Gordon 2001; Seeley and Buhrman 2001; Pratt 2005a; Passino and Seeley 2006a; Visscher 2007; Marshall et al. 2009). For example, Argentine ants, *Iridomyrmex humilis*, are collectively able to find the shortest path to a food source by simply exploiting pheromones while carrying food home (Deneubourg et al. 1990).

The research presented here focuses on collective cognition in the ant *Temnothorax rugatulus* (formerly *Leptothorax rugatulus*) (Formicidae: Myrmicinae) (Figure 1.1). Colonies typically live in fragile rock crevices, and are adept at collectively choosing a new home if their old nest becomes inadequate (Möglich 1978; Mallon, Pratt, and Franks 2001; Visscher 2007). House-hunting in this genus has grown into a leading model system for group cognition, driven by its many practical advantages. First, their colony size is relatively small, ranging from 50 to 250 ants, so it is relatively easy to identify each ant by marking them with unique colors. Second, not only are colonies adept at consistently choosing a favored nest among a group of inferior ones (Visscher, 2007), but individuals are adept as well (Chapter 2). Thus, I was able to assess and compare the cognitive abilities of colonies and individuals. Third, because they achieve such good decisions mainly by a series of observable recruitment behaviors (see below for details), I was able to record how information is transmitted among individuals and link these mechanisms to collective cognitive abilities.

These features have let the house-hunting behavior of *Temnothorax* colonies be well documented (Dornhaus and Franks, 2006; Franks et al., 2003a; Franks et al., 2006; Franks et al., 2003b; Mallon et al., 2001a; Planque et al., 2007a; Pratt, 2005a, 2008; Pratt and Sumpter, 2006; Pratt et al., 2005). Laboratory observation, where individual ants can be easily tracked, has revealed how a colony can select the better of two nest sites, even when few if any individual ants have the opportunity to assess more than one option. Instead, comparison emerges from a competition between recruitment efforts at different sites. The

key elements of this competition are two behavioral rules followed by the scout ants responsible for carrying out the emigration (Figure 1.2a,b). First, if a scout finds a potential new nest, her probability of recruiting nestmates to it depends on the site's quality, as determined by its entrance size, floor area, cavity thickness, light level, and many other features (Mallon et al. 2001). The ants she summons follow the same rule, creating positive feedback that drives up site population at a quality-dependent rate. Second, the scouts accelerate their recruitment once the site population surpasses a threshold. Because better sites are likely to reach the threshold earlier, this quorum rule amplifies the difference in population growth, and the colony is quickly directed towards the best nest (Figure 1.2c,d) (Pratt et al. 2005, Pratt and Sumpter 2006).

In this study, I investigated proximate and ultimate explanations of collective cognition by applying psychology methods and concepts to *Temnothorax* ants. To compare cognition of colonies with that of individuals, I first investigated whether and how well isolated individuals can make decisions (Chapter 2). Then, I explored rationality of decision-making (Appendix B), cognitive capacity (Appendix C) and sensory discrimination (Chapter 3) of individuals and colonies. Finally, I investigated how past experience affects collective decision-making (Chapter 4).



Figure.1.1. *Temnothorax rugatulus* colony showing small colony size and individual marking.

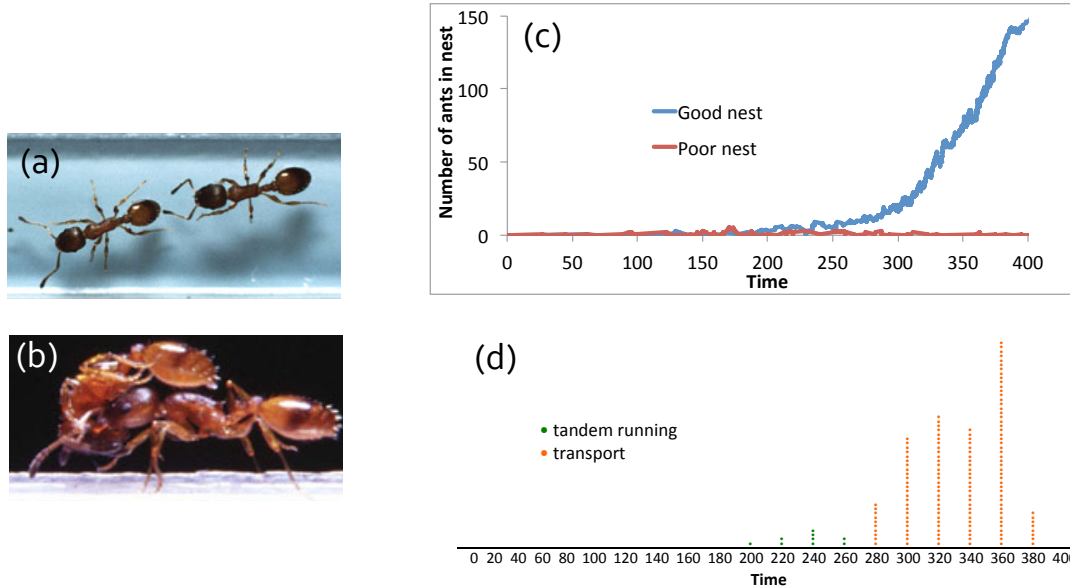


Figure 1.2. (a) Tandem running: a leader attracts a single nest-mate to follow her to the new nest. (b) Transport: recruiter physically carries nest-mates, one at a time. Transport is much faster and more stable than the tandem running. Recruitment behavior switches from tandem-running to transport when the population reaches a certain number, or quorum (c and d). This quorum rule amplifies the difference in population growth, and the colony is quickly directed towards the best nest. The recruitment acts in (d) are all towards the good nest.



## Chapter 2

### INDIVIDUAL ANTS MAKE DIRECT COMPARISON

#### **Abstract**

An optimal decision-making strategy for choosing one among multiple options is to compare them and pick the best. However, this process can be time consuming, especially when the number of options is large. Unlike solitary animals, social insect colonies can manage this trade-off using parallel assessment by multiple individuals. This transfer of comparisons from individual to group raises the question of whether individual social insects have lost the ability to compare options. Past studies have addressed this question in house-hunting *Temnothorax* ants, but their findings were contradictory and inconclusive. In this study, I developed a Markov chain model to predict how often ants should choose a better nest over a poor one under the assumption that they make no comparisons. I estimated the model's parameters from empirical data and compared its predictions to the outcome of actual binary choices made by isolated ants. The results showed that ants chose the better nest more often than predicted, thus indicating that they make comparisons among options. The current trend of "swarm intelligence" assumes that cognition of social insects is fundamentally limited. However, our results suggest that I should never dismiss the remarkable cognition of individual colony members.

#### **Introduction**

Animals often have to choose one among multiple options, such as mates, food sources and habitats. A decision-making strategy for maximizing the fitness

outcome of a choice is to compare all available options and pick the best one among them. However, this process can be time consuming, especially when the number of options is large (Real, 1990). Animals may therefore rely instead on faster heuristics that do not always yield the best option (Gigerenzer and Goldstein 1996; Hutchinson and Gigerenzer 2005). This speed-accuracy trade-off is a common feature of decision-making faced by a wide range of animals (Franks, Dornhaus, et al. 2003a; Marshall et al. 2006; Passino and Seeley 2006a; Ings and Chittka 2008; Chittka, Skorupski, and Raine 2009). For example, when bumblebees faced a color discrimination task on a virtual flower meadow, some bees consistently made rapid but inaccurate decisions while others were slow but accurate (Chittka et al. 2003).

Unlike solitary animals, social insect colonies can manage this trade-off using parallel assessment by multiple individuals. That is, each colony member assesses only one or a few options, and the colony collectively compares all of these assessments to improve its decision quality. For example, when a colony of the ant *Lasius niger* is offered several food sources, each forager typically visits only a single feeder, recruiting nestmates to it with a strength that depends on feeder quality. Through positive feedback, this leads to stronger trails to better sources, with the best source eventually attracting all foragers (Beckers, Deneubourg, and Goss 1992; Gigerenzer and Goldstein 1996; Hutchinson and Gigerenzer 2005). In effect, the act of comparing feeders is distributed across the colony as a whole, without any single ant needing to make a comparison. Similar examples are known from a variety of social insects (Seeley 1986; Beckers et al.

1990; Seeley and Buhrman 1999; Visscher and Camazine 1999; Mallon, Pratt, and Franks 2001; Franks, Dornhaus, et al. 2003a; Marshall et al. 2006; Passino and Seeley 2006a; Ings and Chittka 2008; Chittka, Skorupski, and Raine 2009).

This transfer of comparisons from individual to group raises the question of whether individual social insects have lost the ability to compare options.

Because a colony of social insects divides labor and each member repeatedly performs the same task, only highly specialized abilities might have been selected for (McShea 2000; Anderson and McShea 2001). Thus, social insects might have lost the ability to make comparisons because it is not necessary for collective decision-making. On the other hand, because social insects are morphologically similar to solitary ones, who presumably can make comparisons, it is plausible that individual social insects are also capable of doing so. Individual social insects clearly possess sophisticated cognitive abilities (Gould 1990; Menzel and Giurfa 2001b; Chittka et al. 2003; Collett et al. 2006; Avarguès-Weber, Deisig, and Giurfa 2011). For example, desert ants track their position relative to their home using path integration (Wittlinger, Wehner, and Wolf 2006; Wittlinger, Wehner, and Wolf 2007) and honeybees use waggle dances to convey complex spatial information to their nestmates (Frisch 1993). These findings suggest that cognition of individual social insects is sophisticated enough for them to make comparisons.

These contradictory hypotheses had not been directly tested until ten years ago. Close observations of individual decision-making showed that house-hunting

*Temnothorax* ants are able to make comparisons (Mallon, Pratt, and Franks 2001). Similar to the mechanism of collective decision-making by *Lasius* ants mentioned above, the whole colony can migrate to the best nest among several without individual comparisons (Pratt and Sumpter 2006; Visscher 2007). Mallon et al. (2001) focused on the minority of ants that visited more than one candidate nest and found that these ants were more likely to choose the better nest than predicted if they don't make comparisons. Therefore, they concluded that individual *Temnothorax* ants can make comparisons.

Recently, Robinson *et al.* (2009) argued that these results do not necessarily provide evidence for individual direct comparison. They stressed the adequacy of the emergent mechanism based solely on individual evaluation of a single nest. They assumed that an ant that visits a nest either accepts it and starts recruiting nestmates or rejects it and continues searching. Even if she later returns to a rejected nest, she will treat it as a new discovery. Based on a computer simulation implementing these rules, they concluded that individual comparisons were not required to replicate the results in Mallon et al. (2001).

The status of individual comparison remains unclear, because both of these studies are inconclusive. First, Mallon et al. (2001) looked at colony migrations, where each ant's behavior is influenced by her nestmates. For example, ants dramatically increase their recruitment speed when the population in a candidate new nest reaches a minimum number, or quorum (Pratt et al. 2002; Pratt 2005a). The presence of nestmates might similarly affect an individual's assessment of a

site and thus her probability of recruiting to it. Second, Robinson et al. (2011) did not estimate their model's parameters from empirical data. In particular, they used unrealistically high differences in the likelihood of recruitment to good and poor nests in order to replicate the results of Mallon et al. (2001). Therefore, the results of their simulations may not accurately predict real colony behavior.

In this study, I address both of these issues by making and testing a new model of the behavior of isolated ants. In order to predict how ants should behave if they do not make direct comparisons, the model is "memory-less", meaning that future behavior depends solely on current state. To empirically measure parameters for this model, I first isolated ants from their colonies to avoid confounding social effects from other nestmates. Then, I placed each ant individually in an arena with a few brood items and a single nest, either good or poor. By observing how long it took ants to move the brood into the nest, I estimated their probabilities of accepting each site type. The model based on these empirical data provided an estimate of the probability of ants choosing the better nest in a binary choice if they did not make comparisons. These predictions were then compared to the outcome of actual binary choices using isolated ants. To determine whether ants make comparisons, I tested if the ants showed a higher than predicted probability of choosing the better nest.

## Materials and Methods

### *Markov model of choice behavior*

To predict what would happen if isolated ants do not make direct comparisons, I modeled their behavior as an absorbing Markov chain (Howard 1971; Kemeny and Snell 1976). This approach describes the ant's behavior as a sequence of transitions among a limited number of discrete states. Its main assumption is that each transition depends only on the current state.

When ants choose between two nests, they typically visit both nests multiple times and eventually pick one of them. Thus, our Markov model consists of four states linked by three transition rates (Figure 2.1). These four states are “in good nest”, “in poor nest”, “accept good nest” and “accept poor nest”. In the first two states, ants are in the good/poor nest and assess it. In the last two states, ants decide to accept the good/poor nest and transport brood to it. These accepting states are called absorbing states because individuals are “absorbed” to these states and do not move any further (thus, no arrows are going out from them in Figure 2.1). The three transition rates among these states are acceptance rates, return rates and transition rates. The acceptance rates ( $A_G$  and  $A_P$ ) are the probabilities that an ant in a nest decides to choose that nest as her new home. The return rates ( $R_G$  and  $R_P$ ) are the probabilities that ants leave a nest and come back to the same nest. Finally, the transition ( $T_{GP}$  and  $T_{PG}$ ) rates are the probabilities that they leave a nest and go to the other nest.

I performed experiments to estimate these rates. To obtain the acceptance rates, I introduced one of the target nests, a good or poor one (single choice treatment), and counted the number of visits before the new nest was finally accepted. Each target nest's acceptance rate is the inverse of the average number of visits across individuals. To obtain the return rates and the transition rates, I introduced both the good and poor nests (binary choice treatment). I counted the number of visits for each ant. The return rates and transition rates are inverses of these numbers.

Because the ants often visit both nests multiple times and eventually accept one of them, this Markov chain allows us to calculate how likely ants would choose a good nest over a poor one if they do not make direct comparisons (Table 2.1). Then I compared this probability based on the Markov chain with the one that I obtained in the binary treatment for ants. I tested this with a  $\chi^2$  test of independence by comparing the expected and empirical data of the proportion of choosing the better nest. If ants make a comparison, the probability of choosing the better nest should be higher in the empirical data than in the estimated one.

### *Nest designs*

Each subject was required to start from a home nest and then choose one of two target nests. The three kinds of nests were identical except for their entrance size. The home nest had a mediocre entrance size ( $\phi=3.2$  mm). The better target nest had a smaller entrance size ( $\phi=2.0$  mm), and thus was preferable to the poorer target nest ( $\phi=5.5$  mm) since *Temnothorax* ants strongly prefer

smaller entrances (Pratt and Pierce 2001; Franks, Mallon, et al. 2003b; Pratt 2005a). The roof and floor of the nest were made of glass microscope slides (50 x 75 mm). An entrance was made by drilling a hole in the center of the roof. The cavity was constructed from a balsa wood slat (2.4 mm thickness) with a circular hole (38.1 mm diameter) drilled through its center.

### *Test subjects*

The subjects were 50 individual ants taken from 23 colonies of *Temnothorax rugatulus*. In other *Temnothorax* species, only a minority of a colony's workers participate actively in nest site selection (Mallon, Pratt, and Franks 2001; Pratt et al. 2002; Pratt 2005a). These ants search for and assess sites, recruit fellow scouts, and transport brood items and non-scouts to the chosen site. I assumed that a similar pattern holds in *T. rugatulus* and took steps to ensure that I tested only these active scouts. Since emigration requires scouts to carry brood to the new home, I put brood items outside of the nest and selected as subjects those ants that retrieved them.

All colonies were collected in the Pinal Mountains near Globe, AZ, and were queenright, with worker populations ranging from 100 to 250 and brood populations ranging from 100 to 200. Colonies were housed in a plastic box (11 x 11 cm) with Fluon-coated walls to prevent the ants from escaping. Each box contained a water-filled plastic tube capped with cotton and an agar-based diet (Bhatkar and Whitcomb 1970).



## *Procedure*

### *Single choice experiment*

To estimate the acceptance rates ( $A_G$  and  $A_P$ ) in the Markov Chain formula, I introduced a single target nest, either a good or poor nest, to individual ants and then calculated the probability that each ant accepts the target nest as their new nest.

A home nest was introduced to the shorter wall of the experiment arena (17.8 x 12.7 cm). Along with this nest, two brood items were placed outside of the home nest's entrance. I introduced one individual ant into the arena. I waited for 12 hours, and most individual ants (82%) put the brood items inside the nest during this time period. Thus, I can safely conclude that that she experienced the home nest. Then a target nest was placed near the center of the opposite wall. The roof of the home nest was removed to induce her to move the brood items to the target nest. I videotaped this process for 24 hours, and 91% of ants completed the task within this time period. From this record, to estimate an acceptance rate for each nest, I first counted the number of visits ants made to a target nest before they carried brood items to it. I then took the inverse of this number for each ant. I estimated the acceptance rate as the average of these inverses over all ants.

Each ant was tested only once. Blue plastic sheets were placed underneath all the nests to make brood more visible in the video recordings. The walls of the arena were coated with Fluon. Arenas were illuminated by two LED light panels

mounted on walls 36 cm above the nest, and the ambient level just outside the nest was approximately 115 lux.

### *Binary choice experiment*

To estimate the probability that ants actually choose the good nest over the poor one, I introduced both good and bad nests to them. From the same data, I also estimated the return rates ( $R_G$  and  $R_P$ ) and transition rates ( $T_{GP}$  and  $T_{PG}$ ) for our Markov model by calculating the probability that each ant moved from one nest to the same nest and the probability that they moved from one nest to the other nest.

The methods of this experiment were identical to the single nest experiment except that I introduced both target nests to the arena. 81% of test subjects put the brood items inside the home nest within 12 hours. Then, the roof of the home nest was removed to induce the ant to move the brood items to one of the target nests. I videotaped this process for 24 hours, and 83% of ants completed the task within this time period. From this record, to estimate the return rates, I first counted the numbers of visits to the same target nest until the ant chose a nest. I then took the inverse of this number for each ant. I estimated the return rate as the average of these inverses over all ants. A similar procedure was used to estimate transition rates by counting numbers of visits to the other nest.

## Results

The Markov model, using parameter values estimated from data (Table 2.2) predicts that 63% of ants should choose the good nest if they do not make direct comparisons between sites (Table 2.3). This corresponds to 15.1 of the 24 subjects. In fact, 21 subjects (86%) chose the good nest over the poor one (Table 2.3). This proportion is significantly higher than predicted by the Markov model ( $\chi^2 = 6.31$ ,  $df = 1$ ,  $N = 24$ ,  $p = 0.012$ ), leading us to reject the null hypothesis that ants do not make direct comparisons.

The estimated acceptance rate for the good nest ( $A_G$ ) is roughly 1.5 times higher than that for the poor nest ( $A_P$ ), consistent with past research showing that ants more likely visit and accept a good nest than a poor one (Pratt 2005a; Robinson et al. 2009). The return rates ( $R_G$  and  $R_P$ ) are similar to each other, as are the transition rates ( $T_{GP}$  and  $T_{PG}$ ), although visits to the good nest are slightly more frequent than to the poor one (i.e.  $R_G > R_P$  and  $T_{GP} > T_{PG}$ ).

## Discussion

Algorithms for collective decision-making in social insects typically assume the absence of individual comparisons (Bonabeau, Dorigo, and Theraulaz 1999; Bonabeau, Dorigo, and Theraulaz 2000; Dorigo, Bonabeau, and Theraulaz 2000), but it is rare for this assumption to be empirically tested. An exception is house-hunting by *Temnothorax* ants, where two past studies have directly investigated the existence of individual comparison. Nevertheless, these results are inconsistent: one study showed they do make comparisons (Mallon, Pratt,

and Franks 2001) while another showed that they do not (Robinson et al. 2009). Because these studies examined individual comparisons during colony migrations, interactions with other colony members might affect their assessments. In our experiment, to avoid potential influence by other nestmates, I isolated them from each other and individually tested them. Our results strongly indicate that the individual ants in fact make direct comparisons. I used a mathematical tool, the absorbing Markov chain, to estimate how likely ants would choose the better nest if they do not make direct comparisons. The displayed tendency for the ants to choose the better nest significantly exceeded this estimate. In other words, ants do not independently assess nests, but instead they remember the quality of at least one nest site and compare it to future nests. Our finding that *Temnothorax* individual ants can make comparisons is consistent with the suggestions of several recent studies. For instance, nest site decisions by isolated *T. rugatulus* violate a principle of rational choice called Independence from Irrelevant Alternatives (Appendix B). In that experiment, the preference between two nest sites was altered by a third site, which was less preferred than the first two sites. These decoy effects imply direct comparisons among options (Beckers, Deneubourg, and Goss 1992; Gigerenzer and Goldstein 1996; Bateson and Healy 2005; Hutchinson and Gigerenzer 2005), suggesting that this is the mechanism these ants use to make decisions. Furthermore, individual ants experience cognitive overload (Appendix C), in which the quality of a decision is impaired by a large number of options (M Schroder, J Driver, and Streufert 1967; McShea 2000; Anderson and McShea 2001; Schwartz 2004). Since this

phenomenon is a consequence of decision makers processing too much information, it is likely that these individuals are attempting to compare the many nest sites they are faced with. Finally, central to assuming that ants cannot make direct comparisons is the implication that they do not have memory for potential nest sites. However, a recent study demonstrated that ants can remember the quality and location of potential nest sites encountered before migrations, an ability that contributes to faster and more accurate decisions (Gould 1990; Menzel and Giurfa 2001b; Chittka et al. 2003; Collett et al. 2006; Stroeymeyt, Giurfa, and Franks 2010; Avarguès-Weber, Deisig, and Giurfa 2011).

Why did Robinson et al. (2009) not observe individual comparisons? In their experiment, they observed only 13 ants that visited both the good and poor nests. Because these informed ants did not choose the better site more often than expected by chance, they concluded that ants do not make direct comparisons. However, this claim is weakened by their small sample size, which could yield insufficient power to detect a real effect.

Although our results show that individuals can make comparisons, I still do not know how important this ability is to a colony's decision-making. Because a majority of ants do not have an opportunity to do so during migrations (Mallon, Pratt, and Franks 2001), this ability may have little impact on collective decisions. On the other hand, although only a small portion of ants makes comparisons, their presence might substantially improve colony decision-making. For example, laboratory experiments show that colony members sometimes split among

several nest sites, but that they often eventually merge at the best site. If they were not able to compare their own new home sites with others, it would be hard to resolve these colony splits. Finally, a computer model of *Temnothorax* nest choice predicts that direct comparisons by colony members dramatically improves the quality of their colony decision-making (Marshall et al. 2006). Future research will be needed to explore the impact of the ability of individual comparison on collective decisions.

Recently, many researchers in biology as well as mathematics, computer sciences and others, have been interested in group decision-making in social insects because sophisticated colony cognition emerges from simple individuals. As a result, it is sometimes assumed that ants' cognition is fundamentally very limited. However, our results support the notion that individual insects also have sophisticated cognition (Seeley 2002). The current trend of "swarm intelligence" should never dismiss the remarkable cognition of individual colony members.

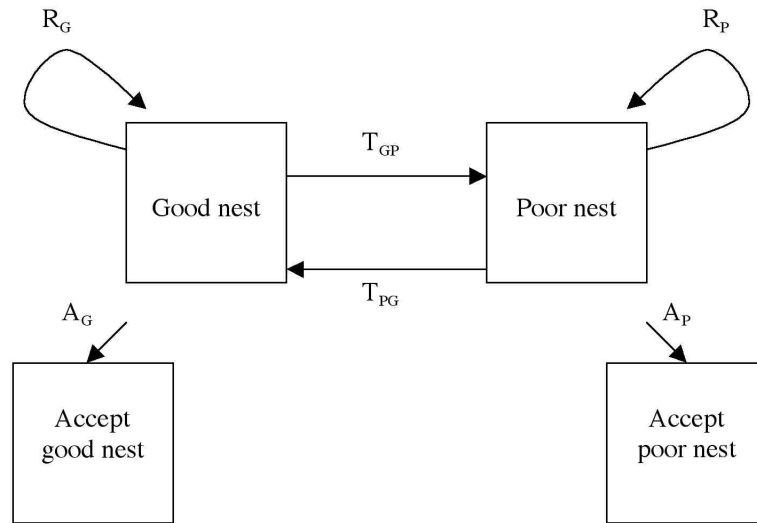


Figure 2.1. Markov chain process for choice behavior. Each box is a discrete state and each parameter is a transition probability. Arrows indicate possible transitions. Because transition probabilities depend only on the current state, this process is “memoryless”.

Table 2.1. Markov model matrix for choice behavior. Each number is a probability of transiting from the current state (row) to the next state (column)

		Next State			
		Good	Poor	Accept Good	Accept Poor
Current State	Good	$R_G$	$T_{GP}$	$A_G$	0
	Poor	$T_{PG}$	$R_P$	0	$A_P$
	Accept Good	0	0	1	0
	Accept Poor	0	0	0	1



Table 2.2. Parameters for the Markov model. The parameters  $A_G$  and  $A_P$  were obtained from the single choice experiment while the others ( $R_G$ ,  $R_P$ ,  $T_{GP}$ , and  $T_{PG}$ ) were from the binary choice experiment. Please see the text for details of the estimation procedure.

$A_G$	$A_P$	$R_G$	$R_P$	$T_{GP}$	$R_{PG}$
0.13	0.08	0.41	0.39	0.46	0.53

Table 2.3. Expected and actual frequencies of choices for good and bad nests

	choice	
	Good	Poor
Expected	15.05	8.95
Data	21.00	3.00

## Chapter 3

### A CROWD IS WISE FOR HARD TASKS BUT NOT FOR EASY ONES

#### **Abstract**

“Collective intelligence” and “wisdom of crowds” refer to situations where groups achieve more accurate perception and better decisions than solitary agents (Franks et al. 2002; Conradt and Roper 2005; Surowiecki 2005; Biro et al. 2006; Ward et al. 2008; Couzin 2009; Krause, Ruxton, and Krause 2010; Woolley et al. 2010; Sasaki and Pratt 2012). Whether groups outperform individuals should depend on the kind of task and its difficulty (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Sasaki and Pratt 2011; Sasaki and Pratt 2012), but the nature of this relationship remains unknown (Conradt and Roper 2005; Couzin 2009; Sasaki and Pratt 2012). Here I show that colonies of *Temnothorax* ants outperform individuals for a difficult perception task, but that individuals do better than groups when the task is easy. Subjects were required to choose the better of two nest sites as the quality difference was varied. For small differences, colonies were more likely than isolated ants to choose the better site, but this relationship was reversed for large differences. I explain these results using a mathematical model, which shows that positive feedback between group members effectively integrates information and sharpens the discrimination of fine differences. When the task is easier the same positive feedback can lock the colony into a suboptimal choice. These results suggest the conditions under which crowds do or do not become wise.

## Introduction

In many taxa, from bacteria to humans, individuals cooperate to evaluate their environment and make collective decisions (Nakagaki, Yamada, and Tóth 2000; Ward et al. 2008; Couzin 2009; Woolley et al. 2010; Sasaki and Pratt 2011). By combining multiple assessments, these groups attain more precise estimates and make more accurate decisions than solitary animals (Fechner, Adler, and Howes 1966; Gescheider 1997; Surowiecki 2005; Krause, Ruxton, and Krause 2010; Seeley 2010). For example, when many diverse individuals independently guess a quantity (e.g. the number of marbles in a jar or the weight of an ox), the group's average estimate is often close to the actual value (Galton 1907; Chittka et al. 2001; Dyer and Chittka 2004; King and Cowlshaw 2007; Dyer, Spaethe, and Prack 2008; Lorenz et al. 2011). Similarly, groups of fish can better distinguish between stimuli than individuals (Ward et al. 2008), and pairs of homing pigeons take more efficient routes than solitary birds (Biro et al. 2006). Condorcet's Jury Theorem and the Central Limit Theorem show that the accuracy of a group of independent decision-makers improves with group size (Condorcet 1785; Hamilton 1967; Wallraff 1978; Simons 2004; Sumpter 2010).

Although wisdom of crowds has both empirical and theoretical support, many examples of collective failure have been documented (Kerr and Tindale 2004; Krause, Ruxton, and Krause 2010; Bahrami et al. 2012). People in groups sometimes arrive at absurd decisions they would not likely make on their own (Janis 1972; Franks et al. 2002; Conradt and Roper 2005; Surowiecki 2005; Ward et al. 2008; Couzin 2009; Sasaki and Pratt 2012). Collectives fail even in

estimation tasks, where they should be especially good at filtering out random errors made by individual members (Sherman and Visscher 2002; Dornhaus and Chittka 2004; Lorenz et al. 2011; Sasaki and Pratt 2011; Sasaki and Pratt 2012). The problem is that groups often violate the assumption of independent decision-making that is central to the wisdom of crowds (Janis 1972; Conradt and Roper 2005; Ward et al. 2008; Couzin 2009; Sasaki and Pratt 2012). Theories assume that individual assessments are made in isolation, and then integrated by a centralized process such as vote counting or averaging. Real groups instead rely on decentralized mechanisms in which interactions and positive feedback bring the group to consensus (Nakagaki, Yamada, and Tóth 2000; Conradt and Roper 2005; Detrain and Deneubourg 2006; Ward et al. 2008; Couzin 2009; Woolley et al. 2010; Sasaki and Pratt 2011; Dussutour, Fourcassié, and Jeanson 2012). These interactions may either improve intelligence by integrating multiple assessments, or hurt it by amplifying mistakes. Understanding which outcome will happen requires a comparison between individual and group performance across a range of challenges.

House-hunting by *Temnothorax* ants provides an excellent model system for this approach (Fechner, Adler, and Howes 1966; Gescheider 1997; Mallon, Pratt, and Franks 2001; Franks, Dornhaus, et al. 2003a; Franks, Mallon, et al. 2003b; Pratt, Sumpter, and Mallon 2005; Surowiecki 2005; Pratt 2005a; Dornhaus and Franks 2006; Pratt 2008; Krause, Ruxton, and Krause 2010; Seeley 2010). Colonies are able to select the better of two nest sites, even when few if any individual ants have the opportunity to assess more than one option (Galton 1907; Chittka et al.

2001; Mallon, Pratt, and Franks 2001; Dyer and Chittka 2004; King and Cowlshaw 2007; Dyer, Spaethe, and Prack 2008; Lorenz et al. 2011). A collective decision instead emerges from a competition between recruitment efforts at different sites (Franks et al. 2002; Ward et al. 2008). At the same time, if ants are experimentally isolated, they can still distinguish two sites of different quality, allowing the decision-making of individuals to be compared with that of colonies (Biro et al. 2006; Sasaki and Pratt 2011; Sasaki and Pratt 2012). This approach has shown that colonies can effectively compare a larger option set than individuals (Condorcet 1785; Hamilton 1967; Wallraff 1978; Simons 2004; Sumpter 2010; Sasaki and Pratt 2012), and that they are less vulnerable to irrational preference shifts induced by decoys (Kerr and Tindale 2004; Krause, Ruxton, and Krause 2010; Sasaki and Pratt 2011; Bahrami et al. 2012). No study, however, has determined how group advantage varies as the difficulty of the task changes.

To address this issue, I adapted psychophysical methods typically used to study sensory discrimination in individual humans or animals (Fechner, Adler, and Howes 1966; Gescheider 1997) (Chittka et al. 2001; Dyer and Chittka 2004; Dyer, Spaethe, and Prack 2008). *Temnothorax rugatulus* subjects (either an individual, a small colony, or a large colony) were given a choice between a constant nest, with a very dim interior light level, and a brighter comparison nest (Figure 3.1). All subjects were expected to prefer the constant nest, because these ants have a strong and unambiguous bias toward darker sites (Franks, Mallon, et al. 2003b; Pratt 2005a). Thus, any choice of the comparison nest could

be taken as a failure to discriminate the options. The brightness of the comparison nest was varied across tests in order to provide an array of challenges of varying difficulty. Discrimination ability was measured in terms of the functional relationship between the brightness of the comparison nest and the probability of choosing the constant nest.

## Results

As expected, both individuals and colonies made more accurate decisions as the choice became easier (Figure 3.2a). However, the shapes of the discrimination curves were quite different. I fitted separate sigmoidal response functions to the colony and individual data:

$$P(\text{correct choice}) = 0.5 + 0.5 \frac{\lambda}{1 + e^{\frac{-(x-\alpha)}{\beta}}} \quad (1)$$

where  $\alpha$  is the discrimination threshold (i.e., the smallest detectable difference in illumination),  $\beta$  is a scale parameter, and  $\lambda$  is the asymptotic level of discrimination (Wichmann and Hill 2001). When the differences were small (i.e. difficult choices), colonies more precisely discriminated options than individuals did. Specifically, the median discrimination threshold  $\alpha$  was 7.4 lux for colonies and 32.3 lux for individuals (Monte Carlo test for  $\alpha_{\text{individual}} > \alpha_{\text{colony}}$ ,  $p = 0.0047$ ). When the choice was easy colonies no longer outperformed individuals, as shown by the higher asymptotic performance of individuals ( $\lambda_{\text{individual}} = 0.93$ ) compared to colonies ( $\lambda_{\text{colony}} = 0.80$ ; Monte Carlo test for  $\lambda_{\text{colony}} < \lambda_{\text{individual}}$ ,  $p = 0.050$ ). Large colonies marginally outperformed small ones across all differences

(Figure 3.2b), but this advantage was not statistically significant (Figure S2 in Appendix A)

To explain these patterns I further investigated the mechanisms by which individual ants make a decision. I first considered the behavior of isolated ants, whose decision-making behavior is relatively poorly understood. By observing lone ants as they chose between two sites of different quality, I established that they make multiple visits to each site, eventually accepting one of them as a new home with a probability that depends on site quality. Furthermore, their probability of choosing correctly grows with the number of times they compare the sites (i.e., visit the two sites in succession; see supplementary materials). Based on these observations I modeled an ant's probability after  $i$  comparisons of accepting the good nest  $A$  or the mediocre nest  $B$ :

$$\begin{aligned} p_A(i) &= q_A \\ p_B(i) &= q_B \left( \frac{2q_B}{q_B + q_A} \right)^i \end{aligned} \quad (2)$$

where  $q_A > q_B$  are the intrinsic qualities of the nests. As well as reproducing the observed increase in acceptance probability with number of visits (Figure S1 in Appendix A), this model implies that the accept probability increases faster when the quality difference between the nests is large. This features reflects the relative ease of distinguishing sites that are very different in quality.



I assumed that a similar process applies to individual ants within intact colonies, but in combination with social information. Colonies rely on a well-described collective mechanism built on three key components: 1) When a scout accepts a site she initiates recruitment of fellow scouts who make their own independent assessment; 2) An ant's probability of initiating recruitment is higher for better sites, leading to differential positive feedback on scout population at the two sites; 3) This difference is amplified by a quorum rule that increases commitment to a site when its population surpasses a threshold. (Franks et al. 2002). I accounted for these rules by expanding the model as follows:

$$\begin{aligned} h_A(i) &= p_A(i) + c \frac{N_A^2}{N_A^2 + T^2} \\ h_B(i) &= p_B(i) + c \frac{N_B^2}{N_B^2 + T^2} \end{aligned} \quad (3)$$

where  $h_{A(i)}$  and  $h_{B(i)}$  give the individual probabilities of accepting a site after  $i$  comparisons,  $N_A$  and  $N_B$  are the number of ants in the two nests, and  $T$  determines the population at which a quorum is reached and the probability of commitment increases sharply (Sumpter and Pratt 2009). The parameter  $c$  determines the relative weighting of individual assessment and social information ( $c = 0$  for solitary ants). A full description of the model along with all parameter values is provided in the supplementary material. When the model was used to simulate the nest discrimination experiment, the output matched our observation

that both individuals and colonies become more accurate as the choice becomes easier (Figure 3.3).

More interestingly, the model showed the distinctive crossing of discrimination curves seen in the data, with colonies doing better at difficult choices and individuals doing better for easier ones (compare Figure 3.2 and Figure 3.3). In order to further test this prediction, I gathered more data for choices involving comparison stimuli on either side of the crossing point observed in the first experiment (Figure S3 in Appendix A). Adding these data and refitting equation 1 gave revised discrimination thresholds  $\alpha_{\text{colony}} = 6.6$  lux and  $\alpha_{\text{individual}} = 30.9$  lux, and saturation levels  $\lambda_{\text{colony}} = 0.78$  and  $\lambda_{\text{individual}} = 0.89$ . These data provided even stronger support for the better performance of groups on difficult tasks ( $p = 0.0020$ ) and similar results for the better performance of individuals on easy tasks ( $p = 0.052$ ).

## Discussion

Our empirical results show the wisdom of crowds for difficult decisions, but the opposite effect when decisions are easy. The model suggests that the reason lies in the different mechanisms employed by individuals and colonies when assessing options. For a difficult choice, solitary individuals have a relatively high probability of accepting the worse nest, because they rely on quality-dependent acceptance probabilities that differ little for similar nests. Successive comparisons cause these probabilities to diverge, but the ant is likely to make her decision before this slow process has had much effect. In whole colonies, on the

other hand, positive feedback and the quorum rule quickly amplify the difference in acceptance rates, allowing the colony to settle on the better site more frequently. As the decision becomes easier, however, acceptance probabilities diverge more rapidly with comparison, allowing solitary ants to reach the right choice with high probability. Studies in honeybees have shown that social interactions do not always improve collective foraging, depending on the distribution of food (Sherman and Visscher 2002; Dornhaus and Chittka 2004). Our study confirms this point and further demonstrates that these interactions sometimes even lower collective performance. This happens when random fluctuations yield a quorum for the inferior nest, locking the colony onto the wrong choice.

The colony's decentralized mechanism sacrifices some level of accuracy in order to make a more rapid decision (Marshall et al. 2006; Passino and Seeley 2006b; Chittka, Skorupski, and Raine 2009; Marshall et al. 2009). Our model predicts such a tradeoff for easier choices, with greater individual accuracy coming at the cost of much slower decision-making. This is consistent with the observation that individuals take much longer to arrive at a decision than is typical for colonies (Supplemental material). However, there is not always a speed-accuracy tradeoff (Sumpter, Zabzina, and Nicolis 2012). When the choice is difficult, by sharing the burden of nest assessment, colonies make decisions both faster and more accurately (Figure S8 in Appendix A).

While the wisdom of crowds has been acknowledged for decades, its failure or “madness of crowds” (Mackay 1841), has been recognized for even longer (Kerr and Tindale 2004). Our work suggests that “madness” and “wisdom” are inescapably entwined. Enhanced group cognition is a clear benefit of living together (Condorcet 1785; Hamilton 1967; Wallraff 1978; Simons 2004; Sumpter 2010), but in situations where decision-making should be straight forward there is a cost to relying on the judgment of others.

## **Materials and Methods**

### *Nest designs*

To measure decision-making performance, I offered subjects binary choices between two kinds of nest: a constant nest and a comparison nest. The constant nest was the same in all choices, with an interior light level of 1 lux. The comparison nest was always brighter than the constant nest, but its specific light level was varied across trials (7, 14, 20, 28, 39, 56 or 112 lux). Each nest was made from a balsa wood slat (2.4 mm thick) sandwiched between glass microscope slides (50 x 75 mm). A circular cavity (38 mm diameter) was cut through the middle of the slat, and a 2mm entrance opening was cut out of the side of the nest (Figure S1 in Appendix A). The floor of the cavity consisted of a single glass slide, while the roof was made from two stacked slides. Interior illumination was adjusted by placing transparent neutral density filters (Rosco Cinegel) between the two roof slides. This design prevented ants from directly contacting the filters, which can sometimes build up an electrostatic charge that

the ants find repellent. Nests were illuminated by two fluorescent light fixtures suspended 37 cm above the bench on which all experiments were carried out. This provided even illumination of 1400 lux at the benchtop, as measured by a Lutron LX-101A light meter. Each fixture had a single 8000°K T-8 full-spectrum daylight bulb (All-Glass Aquarium).

### *Subjects*

Thirty-two colonies of *Temnothorax rugatulus* were used for the colony-level tests. Half of them were small (20-80 workers) and half were large (150-250 workers). An additional 8 medium-size colonies (100-130 workers) provided 16 worker ants (two ants per colony) for the individual tests. Only a minority of workers in *Temnothorax* colonies participate actively in nest-site scouting and transport of nestmates and brood items, while the rest of the colony waits at the home nest (Mallon, Pratt, and Franks 2001; Pratt 2005b). In order to ensure that I tested only these active ants, I placed brood items outside of the colony's nest and selected workers that attempted to retrieve them. I reasoned that ants willing to leave the nest and retrieve brood were likely to carry out similar tasks during colony emigrations (Sasaki and Pratt 2011).

Colonies were collected in the Pinal Mountains near Globe, Arizona (N 33° 19.00', N 110° 52.56', W). All had at least one queen, with worker populations ranging from 20 to 250 and brood populations ranging from 20 to 280. I estimate that 25 to 100 ants (one third of each colony's worker population) actively participated in scouting, site assessment, and recruitment (Pinter-Wollman et al. 2012). Each colony was housed in a nest like those described above, but without

any light filters. Each nest was kept in a plastic box (11 cm x 11 cm), the walls of which were coated with Fluon to prevent the ants from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (Bhatkar and Whitcomb 1970).

### *Experimental procedure*

In each test, a subject (either an individual or a colony) was made to choose between a constant nest and a comparison nest. The comparison nest was always brighter than the constant nest, but its exact brightness varied across tests in order to provide an array of challenges of varying difficulty. Each subject was tested once for each of the seven comparison nests. The sequence of comparisons was varied across subjects to control for order effects. Four distinct orderings were used, with equal numbers of subjects assigned to each (Table 1S in Appendix A).

Tests of individuals began with placement of a home nest against one wall of a rectangular plastic arena (17.8 x 12.7 cm) with Fluon-coated walls. Two brood items were deposited just outside the nest entrance and a single ant was placed in the arena. The ant was then given 12 hours to find the nest and to move the brood inside. This procedure ensured that the subject was aware of both the home nest and the brood items. Constant and comparison nests were then placed against the arena wall opposite from the home. To induce a move to one of these nests, the roof of the home nest was removed. The ant's choice was assayed after 12 hours by recording the nest to which she had carried the brood items. Each of 16 individuals was to be tested 7 times (once for each comparison nest); however, two individuals died and one lost her mark (see below) during the experiment. Thus a total of 106 trials were conducted. In all trials, subjects successfully moved the brood items to the home nest, but twelve trials had to be

excluded from further analysis because the subject failed to move to a target nest. Between trials, subjects were returned to their original colony. Each subject was marked with a unique paint drop on its gaster so that it could be identified and retrieved for subsequent trials. Before each experiment, all glass slides were washed in a commercial dishwasher, and the experimental arena was cleaned with ethanol. Balsa slats were made fresh for each experiment and never re-used.

Tests of colonies followed a similar procedure. The colony in its old nest was placed next to a standard home nest in the center of the arena. The roof of the old nest was then removed to induce the colony to move into the home nest. In all cases, colonies finished migrating within 12 hours. Then, target nests were introduced, and the roof of the home nest was removed to force a choice between the targets. The colony's choice was assayed by recording the nest to which a strong majority of colony members ( $> 90\%$ ) migrated. Each of 16 colonies was tested 7 times with different comparison nests, for a total of 112 trials. In 9 trials colonies split and in one trial the colony did not move to either target nest. These ten trials were not included in the analysis. Order effects were controlled as for the individual tests (Table 1S in Appendix A).



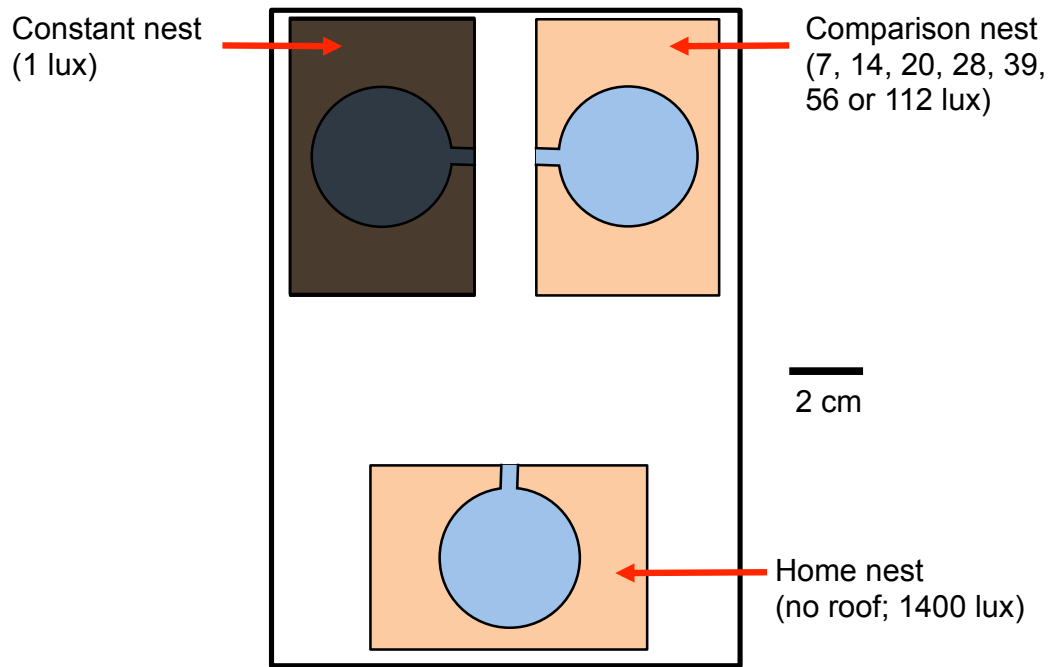


Figure 3.1. Experimental arena for sensory discrimination tests. In each trial, subjects started in the home nest and were induced to choose between the constant and comparison sites. The constant nest was the same in all tests, with a very dim and highly favored interior light level. The comparison nest was always brighter than the constant nest, but its exact brightness varied across tests in order to provide an array of challenges of varying difficulty. Nests consisted of a cavity cut into a wood partition, with a glass ceiling and floor. Cavity light level was modified by adding transparent neutral density filters to the ceiling. Numbers in parentheses indicate interior light levels.

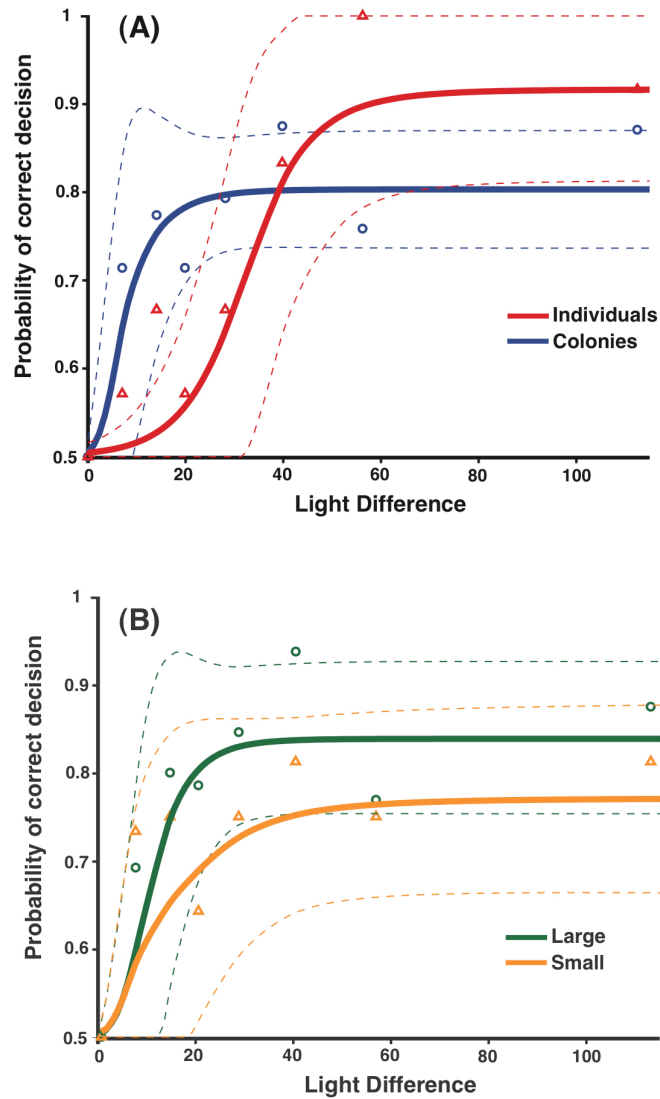


Figure 3.2. The proportion of correct choices made as a function of site illumination difference. (A) Colonies (red triangles) outperform individuals (blue circles) when the illumination difference is small ( $< 40$  lux), but individuals perform better for larger illumination differences. (B) Large colonies (green circles) perform better than small colonies (yellow triangles) over the entire range of tested illumination differences, although this difference is not statistically

significant. Thick lines represent fitting to the psychophysics function specified in equation 1, with parameters sampled from the Bayesian posterior distribution calculated from the data. Dashed lines give 95% confidence intervals.

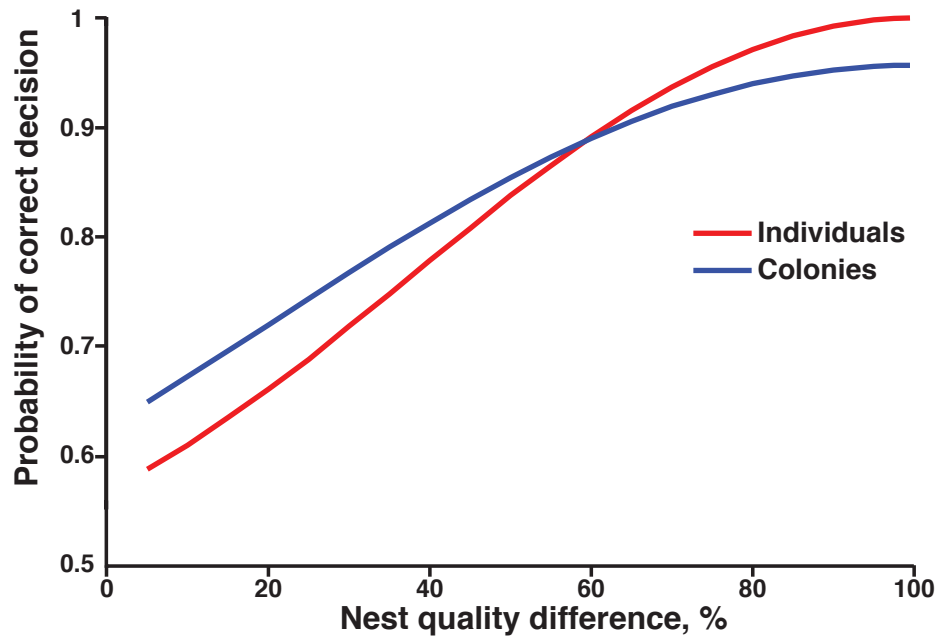


Figure 3.3. Proportion of simulated individuals and colonies (population 100) selecting the better of two nests. Colonies perform better when the quality difference between the nests is small, but individuals choose more accurately when the difference is greater. In the corresponding experiments, a nest's quality is set by its brightness, with darker nests being more attractive. For these simulations,  $q_A=0.20$ , and  $q_B$  varies between 0.20 and 0.001. The quorum parameter  $c=1.1$ .

## Chapter 4

### ANTS ADJUST ATTRIBUTE WEIGHTS ACCORDING TO PRIOR EXPERIENCE

#### **Abstract**

Evolutionary theory predicts that animals act to maximize their fitness when choosing among a set of options, such as what to eat or where to live. Making the best choice is challenging when options vary in multiple attributes, and animals have evolved a variety of heuristics to simplify the task. Many of these involve ranking or weighing attributes according to their importance. However, the importance of attributes can vary across time and place, hence animals might benefit by adjusting weights accordingly. Here I show that colonies of the ant *Temnothorax rugatulus* increase weights on more informative attributes through experience when choosing a nest site. These ants choose their rock crevice nests on the basis of multiple features, including entrance size and interior brightness. After exposure to an environment where one attribute better differentiated options than the other, colonies increased their reliance on the more informative attribute. Although many species show experience-based changes in selectivity based on a single feature, this is the first evidence in animals for adaptive changes in the weighting of multiple attributes. Our studies show that animal collectives, like individuals, change decision-making strategies according to experience. I discuss how collective-level flexibility emerges from individuals.

#### **Introduction**

Evolutionary theory predicts that animals act to maximize their fitness when

choosing among a set of options, such as what to eat or where to live. Decision-making is relatively straightforward for simple options differing in only one attribute. For example, if two flower patches offer honeybees identical nectar but are found at different distances, the closer one, requiring less time and energy to exploit, should clearly be preferred. It becomes more difficult, however, if options vary in multiple ways, especially if no option is superior in all attributes. Thus for honeybees, if flowers offer different qualities and quantities of nectars at different distances, it becomes harder to determine the best choice.

Decision-makers have a variety of ways to handle these situations, but many strategies involve ranking attributes (Payne, Bettman, and Johnson 1993). For example, the weighted additive strategy assigns a weight to each attribute according to its importance. An option's value is determined by summing each attribute score multiplied by its weight, and the option with the highest total score is preferred. This strategy has been observed in many taxa, from insects to humans (Goldstein 1990; Seeley and Buhrman 1999; Franks, Mallon, et al. 2003b). It is often assumed that weights do not change across different contexts (Goldstein 1990). However, because the validity of attributes can vary across time and place, animals might increase their fitness if they adjust weights accordingly (Goldstein 1990; Payne, Bettman, and Johnson 1993; Weber and Borchertding 1993). For example, if bees live in an environment where all flowers have similar nectar quality but very different shapes (and thus different ease of access to nectar), do they learn to weigh shape more than nectar in judging each option?

I tested this hypothesis by studying nest site selection in the ant *Temnothorax rugatulus*. House-hunting in this genus is especially suited to such an analysis, because its nesting criteria and decision-making have been well-studied (Goldstein 1990; Seeley and Buhrman 1999; Mallon, Pratt, and Franks 2001; Franks, Mallon, et al. 2003b; Pratt and Sumpter 2006; Sasaki and Pratt 2012). Colonies typically live in natural cavities, such as fragile rock crevices, and are adept at collectively choosing a new home if their old nest becomes inadequate (Möglich 1978; Goldstein 1990; Pratt and Pierce 2001). Learning plays a role in emigration, with colonies improving their speed over repeated trials (Langridge, Franks, and Sendova-Franks 2004; Langridge, Sendova-Franks, and Franks 2008) and retaining information about the quality of potential new homes in their vicinity (Stroeymeyt, Giurfa, and Franks 2010; Stroeymeyt et al. 2011; Stroeymeyt, Franks, and Giurfa 2011). Most importantly, colonies use a weighted additive strategy that ranks and integrates multiple site attributes, including interior light level, entrance size, and cavity floor area (Franks, Mallon, et al. 2003b).

In this study, I tested whether colonies of *T. rugatulus* adjust attribute weights according to experience. I first determined how a set of colonies weighed interior light level and entrance size, by giving them a choice that traded off these attributes. Then, the colonies were divided into two treatment conditions. In each condition, they repeatedly faced a binary nest choice, but in one treatment the options were distinguished only by entrance size, while in the other treatment they were distinguished only by light level. Finally, all colonies were again given

the original choice to test whether their experience had modified how they weighed the two attributes. If so, I predicted that colonies would increase the weight of the attribute that had been more informative in distinguishing options during the treatment period.

## **Materials and methods**

### *Subjects*

I used sixty colonies of *Temnothorax rugatulus*. All had at least one queen, with worker populations ranging from 128 to 211 and brood populations ranging from 46 to 302. See (Sasaki and Pratt 2011) for details of the collection site and laboratory habitat.

### *Experimental procedure*

To measure how colonies weighed entrance size and interior light level before treatment, I performed binary preference tests between target nests E and L. Nest E had a smaller entrance than nest L (2 mm vs. 5.5 mm), but a brighter interior (525 lux vs. 2 lux). I chose these two attributes because *Temnothorax* colonies show a strong preference for smaller entrances and darker interiors (Pratt and Pierce 2001; Franks, Mallon, et al. 2003b; Pratt 2005a). I designed nests E and L to achieve roughly equal preference at the start (Sasaki and Pratt 2011). That way, I could later detect treatment-induced changes in either direction.

Before receiving the preference test, each colony was first moved from its original nest into a standard home nest with a 3.7 mm entrance and 245 lux light



level. This was done to minimize any effects of current home attributes on site preference (Healey and Pratt 2008). The empty home nest was placed against one wall of a small experimental arena with Fluon-coated walls (17.8 x 12.7 cm). Then, the colony in its original nest was introduced and forced to migrate by removal of the nest's roof. All colonies successfully migrated within 12 hours. The original nest was then taken away and target nests E and L were placed against the arena wall opposite from the home nest. Finally, the roof of the home nest was removed to induce migration. I assayed nest-site preference by recording the site occupied by the colony 12 hours later. Colonies usually showed an unambiguous preference, but they sometimes split between sites. If one site contained over 90% of colony members, including all queens and brood items, I designated that as the colony's choice. If no site achieved this criterion, I did not record a preference. This occurred for only 4 of the 60 colonies.

In the treatment phase, colonies made a series of four choices. In each choice, they chose between one site identical to the standard home nest and another that was inferior to the home nest in one attribute, but identical to it in the other. For half the colonies, the inferior attribute was light level (1400 lux vs. 245 lux in the standard nest); for the other half, the inferior attribute was entrance size (9.5 mm diameter vs. 3.7 mm in the standard nest). Colonies were always expected to choose the standard nest, regardless of treatment. In one treatment, however, this choice would be based on a difference in light level, while in the other it would be based on a difference in entrance size. To avoid any bias due to differences among colonies in how they weight the two attributes, I took account

of their initial preferences when assigning them to treatments. Half of the colonies that chose E were placed in the entrance treatment and the other half in the light treatment. Those that chose L were divided in a similar fashion.

Prior to the first of the four choices, each colony was induced to move into a standard nest, as described above. Each choice usually ended with the colony moving to another standard nest, hence the ants did not have to be re-housed before the next choice. In a few cases (18 of 224 emigrations), they chose the alternative (inferior) nest, and had to be forced to migrate to the standard nest before the next choice, to ensure that all colonies experienced similar contexts during decision-making. In other respects, each choice followed the same procedure used in the initial preference test. Three days elapsed between choices, during which colonies remained in the emigration arena in the presence of the rejected inferior site. This was done to maximize colony exposure to the site, and any associated effects on their weighting of attributes.

Once the treatment phase was complete, colonies were again presented with the original binary choice between sites E and L. This test measured how the treatment had affected the ants' attribute weightings. Specifically, increases in the relative weighting of light level could be detected as an increase in preference for L, while increases in the weighting of entrance size could be detected as an increase in preference for E. Six colonies split either in the pre-treatment or post-treatment tests and so were excluded from further analysis,

leaving a total of 54 colonies. The complete experimental design is shown in Figure 4.1.

### *Nest designs*

Each nest was made from a balsa wood slat sandwiched between glass microscope slides, with a circular cavity cut through the middle of the slat. A nest entrance was drilled through the center of the roof slide. Transparent neutral density filters were used to control the interior illumination. See (Sasaki and Pratt 2011) for further details on nest design and our procedure for preparing and inducing emigrations.

### *Analysis*

To compare preference shifts between conditions, I used a generalized linear model. Post-treatment choice was the response variable, and the treatment condition was a predictor variable. I also included pre-treatment choice as a predictor, in case colonies showed consistent differences in their preferences. I tested the null hypothesis that the preference between targets E and L after the treatment was independent of the type of treatment. The alternative hypothesis was that the two treatment types drive target preference in opposite directions, with E more popular following the entrance condition, and L more popular following the light condition. The statistical package R (v. 2.15.2) was used for all analyses.

## **Results**

In both treatments, colonies shifted their preference toward the site favored by the more informative attribute (Table 4.1). Of the 26 colonies assigned to the

entrance treatment, only 10 chose nest E before the treatment, but this rose to 17 after treatment. Conversely, for the 28 colonies in the light treatment, the number preferring L increased from 16 to 19. A generalized linear model showed a significant effect of treatment on preference (odds ratio = 3.98,  $p = 0.018$ ), but no effect of pre-treatment choice (odds ratio = 0.62,  $p = 0.41$ ). When the model was re-fitted to exclude pre-treatment choice, the odds ratio for treatment was 3.99. This means that the odds of choosing nest E after the entrance treatment (or nest L after the light treatment) were approximately four times greater than the odds of choosing E after the light treatment (or L after the entrance treatment).

## **Discussion**

Our study shows for the first time that animals can change weights on option attributes according to their experience. Specifically, *T. rugatulus* colonies exposed to an environment where one attribute better differentiates options than another increase weighting of the more informative attribute. Past studies on animal decision-making have mainly focused on how experience affects a single attribute, particularly during mate choice (Bakker and Milinski 1991; Collins 1995; Wagner, Smeds, and Wiegmann 2001; Hutchinson 2005). For example, female fruit flies show less interest in intermediate-quality males after exposure to high-quality males than after exposure to low-quality males (Dukas 2005). Studies like this have tested if decision-makers change their selectivity according to the average quality of options available in their environment. I instead created an environment where one attribute was more informative than another and showed

that colonies can adjust attribute weights to emphasize the more informative feature.

Our results cannot easily be explained as a simple result of differing colony state following the two experimental conditions. Such effects are well known in foraging, where different treatments affect the state of the subject and thus its preferences (Schuck-Paim, Pompilio, and Kacelnik 2004). In fact, the quality of the current nest is known to influence emigration behavior by *Temnothorax* ants. Ants make faster moves, and possibly less discriminating choices, when abandoning a good nest that has just been destroyed than when leaving a similarly-treated poor nest (Healey and Pratt 2008). To avoid this effect, I took pains to ensure that colonies lived in identical nests in both the light and entrance size conditions. That is, the better option was always the standard home nest, and the only difference between conditions was the design of the inferior nest, which was rarely chosen. This design allowed us to eliminate any bias caused by the subject state and instead to test how the contrast between options affected later decisions.

Effects of prior experience on attribute weights have previously been explored in humans (Goldstein 1990; Lenton, Fasolo, and Todd 2009). For example, as the range of values taken by an attribute widens, its weight increases (Weber and Borchering 1993). Our results are consistent with these findings. When I varied the quality of one attribute across options but kept the other the same, I found that the attribute with the wider range became more heavily weighted. I further showed that this weight modification persists over time, affecting decisions in a

new environment. Past studies typically exposed subjects to different choice environments and measured weights within these distinct environments. I tested all subjects in a common context, with exactly the same choice set, after exposing them to different environments. Thus, I can conclude that the observed changes in attribute weightings were due to past experience, rather than the environment at the time of choosing.

What could be the benefit of flexible weights? Because the environment can change across time and place, reliability of attributes is not constant.

*Temnothorax* colonies, for example, might find themselves in a dense forest thoroughly covered by a thick canopy and thus uniformly dark, or they might instead live in a younger, more open forest where some areas are much darker than others. Because light level is more important in distinguishing better from worse sites in the latter environment, ants may gain fitness by increasing the weight for this attribute. As another benefit, decisions can be improved by simply ignoring less informative attributes, thus reducing the amount of information that must be considered (Gigerenzer, Todd, and Group 1999). Because decision-making based on multiple attributes is cognitively demanding, larger numbers of attributes can paradoxically lead to cognitive overload and inferior decisions (Schwartz 1986; Sasaki and Pratt 2012). Theories predict and experiments have shown that focusing on only the most important attribute can improve speed and accuracy (Gigerenzer and Goldstein 1996; Gigerenzer and Goldstein 1999), two important factors for animal decision-making (Chittka, Skorupski, and Raine 2009).

Studies on prior experience and decision-making have typically focused on solitary animals (Schuck-Paim, Pompilio, and Kacelnik 2004; Stephens, Brown, and Ydenberg 2008; Shettleworth 2009). Our work shows that experience also matters for collectives, as recent studies showed in *Temnothorax* ants (Healey and Pratt 2008; Langridge, Sendova-Franks, and Franks 2008; Sasaki and Pratt 2011; Stroeymeyt et al. 2011). Unlike solitary animals, social insects typically cooperate to evaluate options and make collective decisions. This leaves open the question of how the colony-level flexibility that I observed emerges from individual behavior. One scenario is that, like the colony, individuals compare the two sites, detect the difference in one attribute, and then change weights accordingly. Alternatively, decision-making strategies might be very different at the individual and collective levels. For example, when individuals encounter a nest with low quality for a particular attribute, they might simply increase the weight for this attribute, known as the scarcity effect in psychology (Worchel, Lee, and Adewole 1975). This strategy would not require direct comparison by individuals, but it would lead to comparison by the colony as a whole. Future work should investigate exactly how experience affects the behavior of individual colony members. Studies such as these will allow us to decipher the underlying mechanism of the collective-level flexibility.

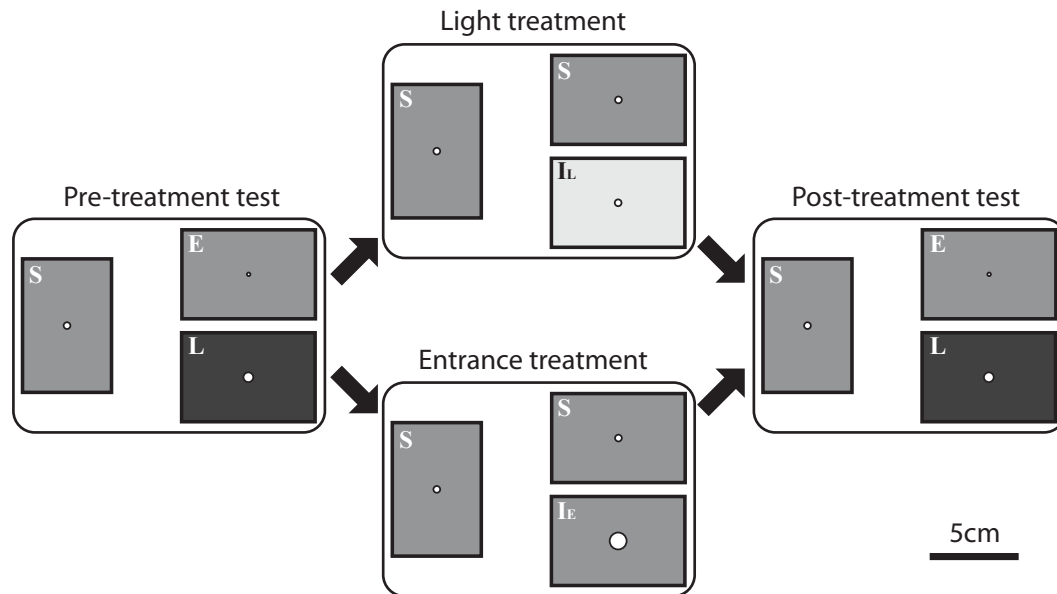


Figure 4.1. Experimental assessment of the effect of experience on attribute weights. An initial binary choice between sites E and L showed how colonies weighted entrance size and interior light level. Colonies then made a series of four choices in which only one attribute provided distinguishing information. In each choice, they chose between a standard nest (S) and another that was inferior to the standard nest in one attribute, but identical to it in the other. For half the colonies, the inferior attribute was light (I<sub>L</sub>); for the other half it was entrance size (I<sub>E</sub>). Finally, colonies repeated the original choice to determine whether experience had altered their preferences.



Table 4.1. Nest site preferences of colonies before and after treatment conditions in which either entrance or light level were informative for decision-making.

Results are shown as contingency tables classifying each colony by its choices before and after treatment. In each treatment, colonies shifted their preference toward the option favored by the more informative attribute. E and L stand for the small entrance nest and the darker nest, respectively.

		<u>Entrance Condition</u>		<u>Light Condition</u>	
<b>After Treatment</b>		<b>Before Treatment</b>		<b>Before Treatment</b>	
		E	L	E	L
	E	6	11	3	6
	L	4	5	9	10

## Chapter 5

### CONCLUSION

This dissertation investigated the ultimate and proximate explanations of collective cognition. At the ultimate level, I compared cognitive abilities of *Temnothorax* colonies and individuals to test whether groups have an advantage. I first confirmed that isolated individuals make decisions by comparing available nests (Chapter 2). This finding allowed me to give the same cognitive tasks to individuals and colonies and directly compare their performance. My studies confirmed superior collective cognition: while individual ants frequently make irrational decisions, colonies are overwhelmingly rational as a whole (Appendix B), colonies have higher information-processing power than individuals (Appendix C), and colonies have more precise sensory discrimination than individuals (Chapter 3). In the study of Chapter 4, however, when the task was easy, individuals actually outperformed colonies.

These results demonstrated novel advantages of group living. It has been shown that individuals can gain benefits in many ways by forming a group (Krause and Ruxton 2002). For example, black-headed gulls capture food more easily when they hunt in flocks than when foraging by themselves (Gotmark, Winkler, and Anderson 1986), a pride of lions can better defend a hunting territory than a single lion can (Packer, Scheel, and Pusey 1990), a cluster of male emperor penguins can conserve their energy much more efficiently than isolated ones (Ancel et al. 1997), and females of lekking species prefer to mate with males in a

group (Wiley 1973). My research shows a very different kind of benefit to group living: improved cognition. Although all my studies were conducted in the laboratory, the superior cognitive abilities of groups should also be beneficial in nature, where nest site selection is likely a frequent and important task for colony survival and reproduction (Möglich 1978; Herbers 1989; Foitzik and Heinze 1998). Future work is required to investigate exactly when and how the collective advantages are used in their natural habitat.

At the proximate level, I investigated the underlying mechanisms of these collective phenomena. I found that colonies achieved rationality (Appendix B) and higher information-processing power (Appendix C) by sharing the burden of nest assessment among members. The mathematical model in Chapter 3 shows that positive feedback between group members effectively integrates information and sharpens discrimination of fine differences. When the task is easier, however, the same positive feedback can lock the colony into a suboptimal choice.

My studies investigated several cognitive tasks, in which collective cognition succeeds or fails. Although collective cognition should theoretically be superior (Condorcet 1785; Simons 2004), many examples of collective failure have been documented (Bahrami et al. 2012). There are at least two problems with the underlying assumptions of the theories. The first problem is that they typically ignore or simplify individual cognitive abilities and conclude that groups always have superior cognition (Bonabeau, Dorigo, and Theraulaz 1999). However, it

has been shown that these abilities are often more complex than assumed (Gould 1990; Menzel and Giurfa 2001b; Seeley 2002). The second problem is that theories assume that individual assessments are made in isolation, and then integrated by a centralized process such as vote counting or averaging. Real groups instead rely on decentralized mechanisms in which interactions and positive feedback bring the group to consensus (Sumpter 2010). The violation of these assumptions suggests that groups may not make better decisions than individuals under certain circumstances. In this dissertation research, I overcame the challenges described above using the house-hunting *Temnothorax* ant, which provides a detailed understanding of individual cognitive abilities and of information transfer among group members.

Recent studies noted the similarities between information processing of a social insect colony and that of the brain (Hofstadter 1999; Passino, Seeley, and Visscher 2008; Marshall and Franks 2009; Mitchell 2009). It has further been suggested that both systems achieve statistically optimal decision-making (Marshall et al. 2009). Emergent processes of individual cognition have been a major topic in many fields, including psychology and biology, but they remain largely unknown. This is partially because neurons are connected in a very complex way and it is hard to untangle or manipulate them. The workers of a social insect colony are, on the other hand, much less tightly integrated. This difference makes it straightforward to isolate individual insects (Chapter 2) and to manipulate colony organization by adding and removing certain individuals (Wilson 1980). By taking advantage of these parallels between a colony and a

brain, future studies can use social insect colonies for deeper understanding of emergent processes of cognition.

One may wonder if I can measure individual cognition by testing isolated social insects, because this unnatural setting may alter their internal states. For example, isolated ants may look for their nestmates instead of new sites, making their site choices arbitrary and worse than that of colonies. However, my studies show that these individuals make consistent decisions, which are as good as or even better than colonies under certain circumstances (Sasaki and Pratt 2011; Sasaki and Pratt 2012; Sasaki et al. 2013). Thus, social insects can efficiently solve cognitive tasks even when they are isolated from their colony members. In fact, much has been learned about individual cognition of social insects by isolating them. Studies of isolated honeybees have made them into a major model system for animal cognition, including, perception, learning, memory and decision-making (Gould 1990; Smith 1993; Menzel and Giurfa 2001b; Wright et al. 2013). Therefore, testing individual cognition of social insects by isolating them is not just a valid but also powerful method.

For over a century, collective cognition has been investigated empirically and theoretically, I still know little of when and how groups make better or worse decisions than individuals. My dissertation research investigated this relatively unexplored question using the house-hunting *Temnothorax* ant. Because these ants can process information both individually and collectively, I was able to directly compare the cognitive abilities of individuals and groups by giving them

the same cognitive tasks. I hope that these techniques and results help the field move forward towards better understanding of collective cognition.

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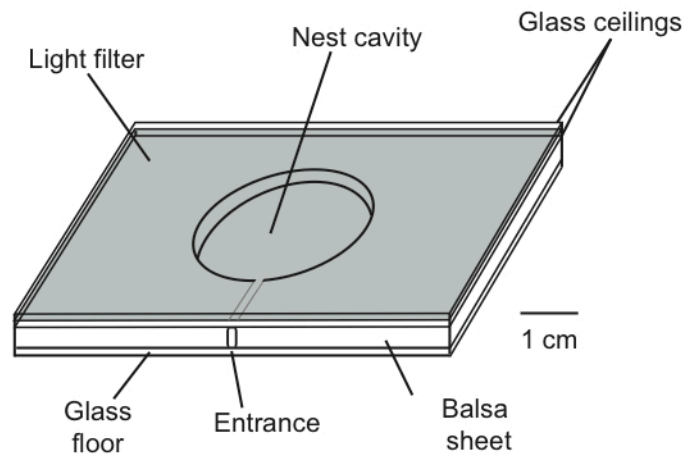
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APPENDIX A

SUPPLEMENTAL MATERIALS FOR CHAPTER 3

## Materials and methods



**Fig. S1.** Nest design used in discrimination experiments.

**Table S1.** Test orderings used in the individual and colony experiments. The number in each cell is the interior light level of the comparison nest (lux). Groups 1 and 2 progressed from mid-range values to more extreme ones, while groups 3 and 4 progressed in the opposite direction. Each group included an equal number of subjects.

	<b>Order in sequence of trials</b>						
	<b>1</b>	<b>2</b>	<b>3</b>	<b>4</b>	<b>5</b>	<b>6</b>	<b>7</b>
<b>Group 1</b>	28	39	20	56	14	7	112
<b>Group 2</b>	28	20	39	56	14	112	7
<b>Group 3</b>	7	112	14	56	20	39	28
<b>Group 4</b>	112	7	56	14	39	20	28

## Fitting the psychophysical function

I fitted a sigmoidal psychophysical function (Equation 1) to the experimental results. I hypothesized that colonies will perform better than individuals at lower illumination differences, but worse at higher differences. This could manifest itself by colonies having a lower threshold  $\alpha$  and a lower asymptotic discrimination level  $\lambda$ . To fit the function I used the data from colonies or individuals to infer the Bayesian posterior distribution of the three model parameters,  $\theta = \{\alpha, \beta, \lambda\}$ .

$$P(\theta|D) = \frac{P(D|\theta)P(\theta)}{P(D)} \quad (S1)$$

Here  $D$  is the data,  $P(D | \theta)$  is the likelihood, calculated using equation 1 applied to each decision, and  $P(\theta)$  is a prior distribution of the possible parameters, which I take as uniform over the range  $([0 \ 0 \ 0], [100 \ 100, \ 1])$ .  $P(D)$  is a normalizing constant that does not need to be calculated.

I acquire samples of parameter values from this posterior distribution using Metropolis-Hastings Markov Chain Monte Carlo (MCMC) sampling (MacKay, 2003; Metropolis, Rosenbluth, Rosenbluth, Teller, & Teller, 1953). This provides 100,000 parameter samples in proportion to the posterior probability of those parameter values. I can use these parameter samples directly to calculate  $P(t_c < t_i | D_c, D_i)$  and  $P(\lambda_c > \lambda_i | D_c, D_i)$ , where  $D_c$  and  $D_i$  are the colony and individual data, respectively. Over 100,000 iterations I pick (with replacement) a random sample from the colony parameter samples and compare it to another randomly picked

sample from the individual samples. I ask in what proportion of cases the above inequalities hold, and calculate our p-value directly from this (Fig. S2). I can also use the parameter samples to produce a 'best fit' curve (thick lines in Fig. 2) to the observed proportions, by summing over the possible parameter values. For example,

$$P(\text{correct choice} \mid D) = \int P(\text{correct choice} \mid \theta) P(\theta \mid D) d\theta \approx \sum_j P(\text{correct choice} \mid \theta_j)$$

where  $\theta_j$  is the  $j$ th parameter sample.

I can also calculate the variance of this estimate and thus provide 95% confidence intervals (dotted lines in Fig. 2). The 'best fit'  $y_c$ , to the colony data is significantly greater (at 5%) than the individual data when

$(y_c - y_i) > 1.64 \sqrt{\text{Var}(y_c) + \text{Var}(y_i)}$ , where 1.64 comes from this being a 1-sided test. The inequality can be reversed to find when  $y_i$  is significantly greater than  $y_c$ .

A similar approach was used to compare the performance of large and small colonies.

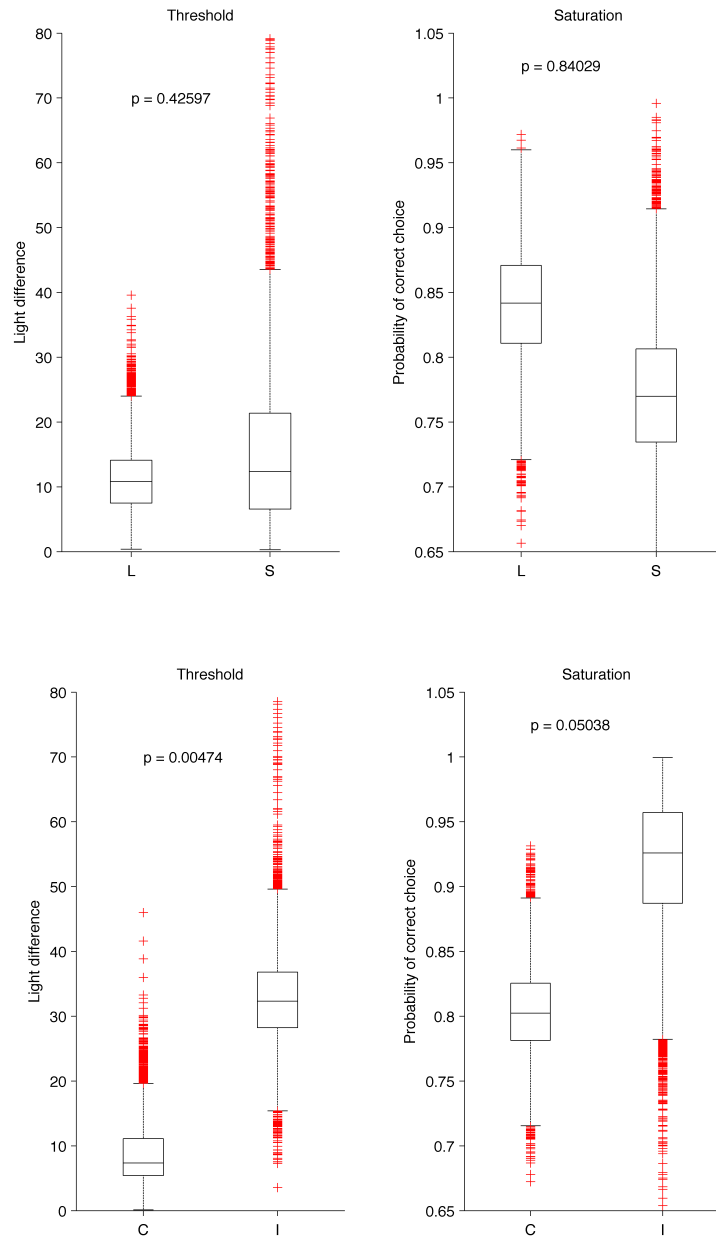


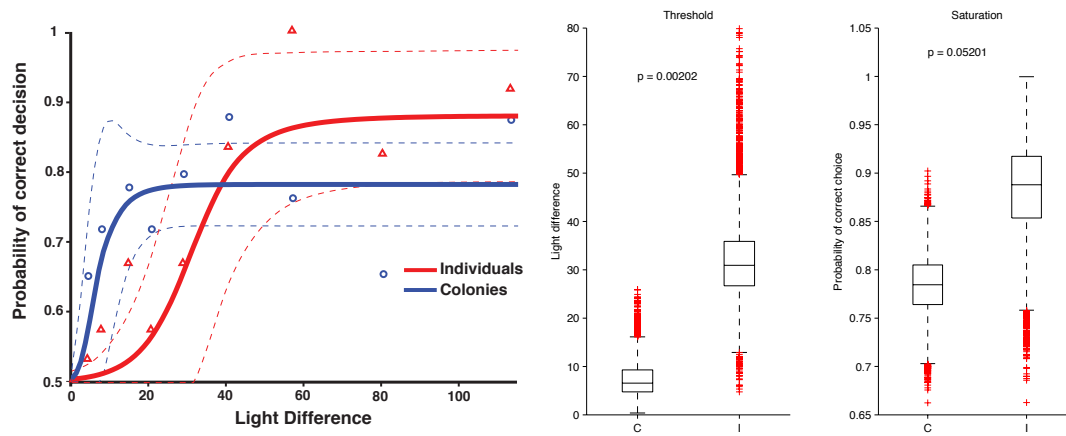
Figure S2. Posterior distribution of the threshold parameter  $\alpha$  and the asymptotic parameter  $\lambda$  of the psychophysical function. Box plots indicate the distribution of parameter samples from Metropolis-Hastings MCMC, fitting equation 1 to the data. (a) Distribution of the threshold parameter,  $\alpha$ , for colonies (C) and individuals (I). Colonies have a lower threshold value, indicating better

performance at low illumination differences. (b) Distribution of the asymptotic parameter  $\lambda$ . Individuals have a higher asymptotic level, indicating better performance for large illumination differences. (c) Distribution of  $\alpha$  for large (L) and small (S) colonies. (d) Distribution of the saturation parameter for large and small colonies. No significant effect of colony size was found for either parameter ( $\lambda_{\text{small}} = 0.77$ ,  $\lambda_{\text{large}} = 0.84$ ; Monte Carlo test for  $\lambda_{\text{large}} < \lambda_{\text{small}}$ ,  $p = 0.84$ ;  $a_{\text{small}} = 12.4$  lux,  $a_{\text{large}} = 10.8$ ; Monte Carlo test for  $a_{\text{large}} < a_{\text{small}}$ ,  $p = 0.43$ ).

## **Testing the model prediction**

To test the model prediction that colonies perform better at difficult choices but individuals do better for easier ones, twenty colonies and twenty individuals were tested for one difficult and one easy choice as additional data points. The experimental procedure was identical to the one described above except that it used different comparison nests: 4 lux and 80 lux in the difficult and easy choices, respectively. Half of the subjects in each group were first tested for the difficult choice and then for the easy choice. The other half were tested in the opposite order. All colonies were medium size, with 90-130 workers. Figure S3 shows the results, which are further described in the main text.





**Fig. S3.** (a) The proportion of correct choices made as a function of site illumination difference, including both the original data and two new data points. (b) The statistical results show even stronger support for the better performance of groups on difficult tasks and similar results for the better performance of individuals on easy tasks.

## Markov chain model

A Markov chain model was used to describe the *Temnothorax* house hunting process. In the model, each ant begins in the Exploring state from which she can find one of the two nests, entering state  $A$ , corresponding to the better nest, or  $B$ , corresponding to the worse nest. If she fails to find either nest, the ant continues exploring. With each subsequent nest visit, the ant enters state  $CA_i$  or  $CB_i$ , where  $i$  represents the number of comparisons she has made between nests. This  $i$  is incremented each time the ant goes from  $A$  to  $B$ , or from  $B$  to  $A$ . At each state the ant has a probability of committing to the nest she is currently assessing. Once she commits to a nest, she enters final state  $a$  or  $b$ . See Table S2 for a summary of model states, Table S3 for the model's transition probabilities, and Table S4 for a description of the model parameters. The flowchart in Figure S4 summarizes all possible state transitions.

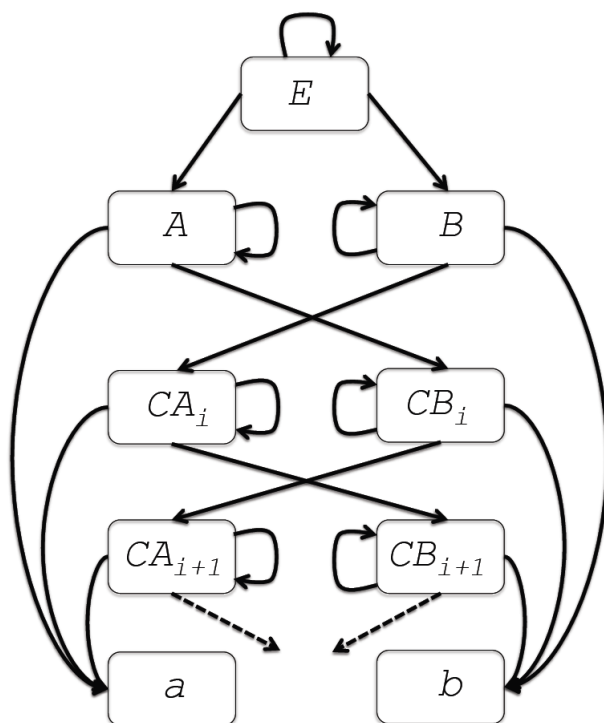
The probability of an ant committing to a particular nest is a function of the nest's intrinsic quality  $q$  and the number of times she has compared it with the other nest (Equation 2). This relationship was based on observations of isolated ants choosing between a good and a mediocre nest. The probability of choosing correctly after multiple nest visits grew with the number of visits (Fig. S5). Under equation 2, the probability of committing to the good nest remains constant, but the probability of committing to the poor nest decreases with each comparison. This assumption implies that the accept probability increases faster when the quality difference between the nests is large. Equation 3 combines this mechanism with the quorum rule employed by ants in the presence of nestmates

(Pratt, Mallon, Sumpter, & Franks, 2002). Under this rule, the probability of committing to a site increases in a step-like way with site population. For the purpose of calculating the populations of each nest ( $N_A$  and  $N_B$ ), I added the number of ants in final state  $a$  to 20% of the ants in states  $A$  and  $CA_i$ . This reflects the approximate percentage of time actually spent by those ants inside the nest, where they can contribute to another ant's assessment of quorum attainment. A colony is considered to have chosen nest  $A$  when more than half of the ants are in state  $a$ .

When simulated in Matlab, the model produced results consistent with those observed in the experiments. Both colonies and individuals improved their performance as the problem became easier. Larger colonies were better able to solve problems for the entire range of difficulty (see Figure S6). For more difficult problems, colonies were able to select the better nest more accurately and faster than individuals. However, for a range of parameter values, individuals were able to outperform colonies for the easiest problems (Fig. 3). The initial ratio of nest qualities and the weight assigned to the quorum factor for colonies both have an effect on the individuals' ability to perform better than colonies in the simulations. When the quorum weight factor  $c$  is high ( $c > 1$ ), colonies get locked into their nest choices very quickly, leading to more suboptimal decisions for the entire range of problem difficulties. For low values of  $c$ , the crowds are always able to outperform individuals (Fig. S7).

Our model further shows a tradeoff between speed and accuracy for easy choices: individuals take longer but make more accurate decisions than colonies.

In contrast, for difficult choices, colonies make decisions both faster and more accurately. Colonies achieve this by sharing the burden of nest assessment among members (Fig. S8).



**Fig. S4.** Summary of all possible states and transitions in the Markov chain model.

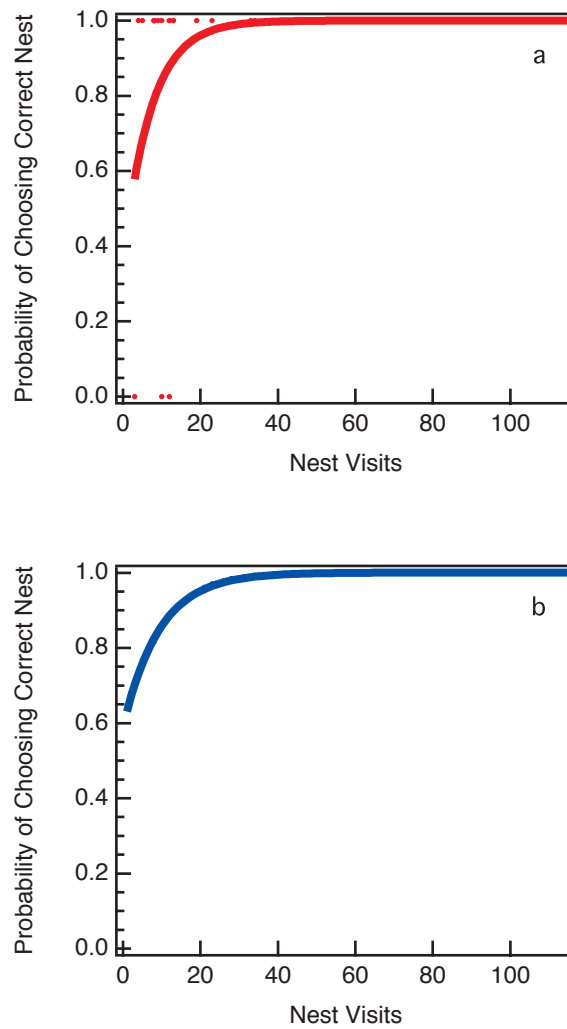


Figure S5. Proportion of individuals choosing the good nest as a function of the number of nest visits they make in the experiments (a) and in the simulation (b). In the model, the particular pair of nests used to generate the figure have  $q_A=0.20$  and  $q_B=0.13$ .

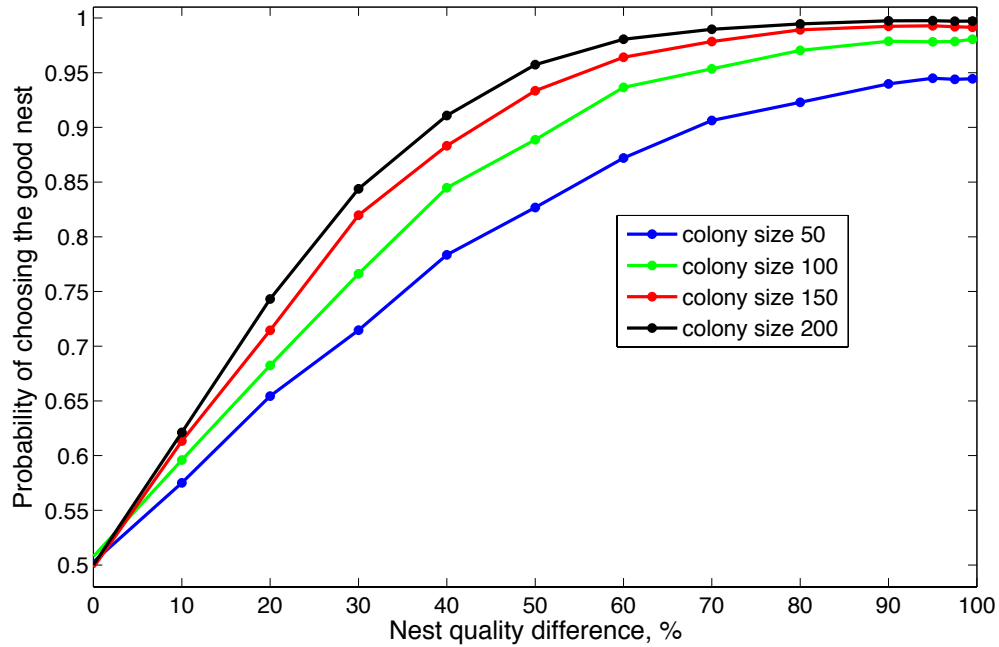


Figure S6. Proportion of individuals and colonies (size 100) selecting the better of two nests in the simulation over 1,000,000 simulation runs. In this figure,  $q_A=0.20$ , and  $q_B$  varies between 0.20 and 0. The quorum parameter  $c=1.1$ . Colonies perform better when the quality difference between the nests is small, but individuals choose more accurately when the difference is greater. In experiments, a nest's quality is expressed by its brightness, with darker nests being more attractive.

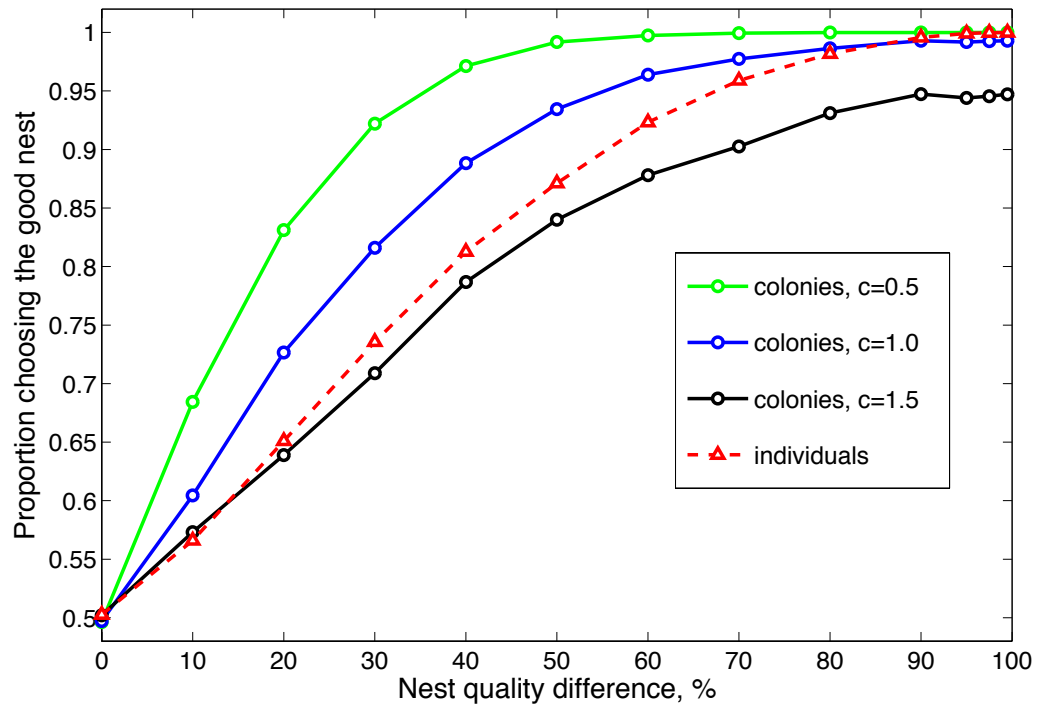


Figure S7. Results of model simulation for different values of parameter  $c$ , controlling the strength of the quorum effect in colonies selecting their nests.



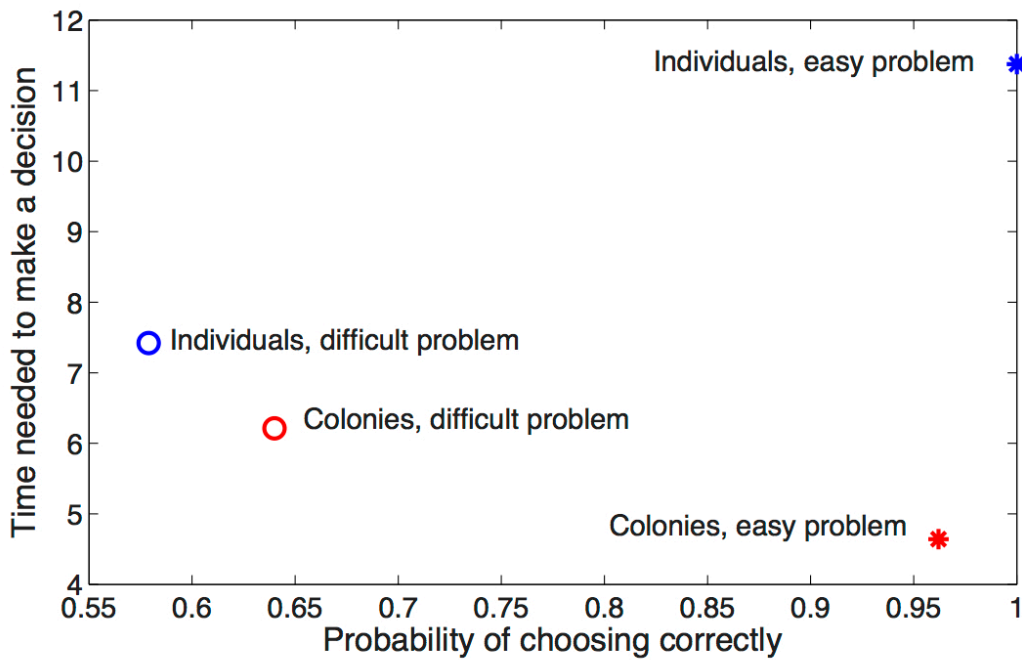


Figure S8. Speed-accuracy trade-off between simulated individuals and colonies (size 100) choosing between two nests given an easy ( $q_A=0.20$ ,  $q_B=0.005$ ) and a difficult ( $q_A=0.20$ ,  $q_B=0.19$ ) problem. For the difficult problem, colonies are able to make their choice faster and with greater accuracy. For the easy problem, the colonies still choose faster, but individuals choose with greater accuracy.

Table S2. States of the Markov chain model.

State	Meaning
$E$	Exploring: no nests visited
$A$	Only nest $A$ has been visited
$B$	Only nest $B$ has been visited
$CA_i$	Both nests have been visited; $i$ comparisons have been made
$CB_i$	Both nests have been visited; $i$ comparisons have been made
$a$	Final state: nest $A$ has been accepted
$b$	Final state: nest $B$ has been accepted

Table S3. Transition matrix of the Markov chain model.

Stat e	E	A	B	CA <sub>1</sub>	CB <sub>1</sub>	CA <sub>2</sub>	CB <sub>2</sub>	...	a	b
E	r	(1-r)f <sub>A</sub>	(1-r)f <sub>B</sub>	0	0	0	0	...	0	0
A	0	(1-g <sub>B</sub> )(1-h <sub>A0</sub> )	0	0	g <sub>B</sub> (1-h <sub>A0</sub> )	0	0	...	h <sub>A</sub> 0	0
B	0	0	(1-g <sub>A</sub> )(1-h <sub>B0</sub> )	g <sub>B</sub> (1-h <sub>B0</sub> )	0	0	0	...	0	h <sub>B</sub> 0
CA <sub>1</sub>	0	0	0	(1-g <sub>B</sub> )(1-h <sub>A1</sub> )	0	0	g <sub>B</sub> (1-h <sub>A1</sub> )	...	h <sub>A</sub> 1	0
CB <sub>1</sub>	0	0	0	0	(1-g <sub>A</sub> )(1-h <sub>B1</sub> )	g <sub>B</sub> (1-h <sub>B1</sub> )	0	...	0	h <sub>B</sub> 1
...	...	...	...	...	...	...	...	...	...	...

Table S4. Markov chain model parameters.

Parameter/ Expression	Meaning/ Value
$i$	Number of comparisons between nests $A$ and $B$
$r$	Probability of not finding either nest from the Exploring state, $r=0.5$
$f_A$	Probability of initially finding nest $A$ , $f_a=0.5$
$f_B$	Probability of initially finding nest $B$ , $f_b=0.5$
$g_A$	Probability of finding nest $A$ from the current nest, $g_a=0.5$
$g_B$	Probability of finding nest $B$ from the current nest, $g_b=0.5$
$q_A$	Quality of nest $A$ , indicated by the initial probability of accepting $A$ , $q_a=0.2$
$q_B$	Quality of nest $B$ , indicated by the initial probability of accepting $A$ , $q_a$ is varied during the simulation to indicate difficulty of choice
$p_A(i)$	Probability of accepting nest $A$ by a single ant after $i$ comparisons of the nests
$p_B(i)$	Probability of accepting nest $B$ by a single ant after $i$ comparisons of the nests
$h_A(i)$	Probability of accepting nest $A$ by an ant after $i$ comparisons, taking into account the quorum effect
$h_B(i)$	Probability of accepting nest $B$ by an ant after $i$ comparisons, taking into account the quorum effect
$N$	Total number of ants in the colony. In the model runs, $N=100$ for small colonies, and $N=200$ for large colonies
$N_A$	Number of ants that have accepted nest $A$
$N_B$	Number of ants that have accepted nest $B$
$T$	Threshold parameter, $T=0.2*N$

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## APPENDIX B

### EMERGENCE OF GROUP RATIONALITY FROM IRRATIONAL INDIVIDUALS

# Emergence of group rationality from irrational individuals

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Evolutionary theory predicts that animal decision makers should be rational, meaning that they consistently choose fitness-maximizing options. Despite this, violations of rationality have been found repeatedly in humans and other animals. The significance of these violations remains controversial, but many explanations point to cognitive limitations that prevent animals from adequately processing the information needed for fully rational choice. Instead, they rely on heuristics that usually work well but yield systematic errors in specific contexts. Although past research on rationality has focused on individuals, many highly integrated groups, such as ant colonies, regularly make consensus choices among food sources, nest sites, or other options. These collective choices emerge from local interactions among many group members, none of whom take on the whole burden of decision making. We hypothesized that groups may evade the irrational consequences of individual limitations by distributing their decision making across many group members. We tested this in the well-studied case of collective nest-site selection by *Temnothorax* ants. We found that individual ants, but not colonies, strongly violated rationality when presented with a challenging nest-site choice. Specifically, isolated individuals irrationally switched their preference between 2 alternative nest sites based on their experience of an unattractive decoy. Given the same choice, intact colonies maintained consistent preferences regardless of the decoy's presence. Previous studies have stressed how distributed decision making can filter out random errors made by group members. Our results show that collectives can also suppress systematic errors that emerge from the decision heuristics of cognitively limited individuals. **Key words:** collective cognition, dynamic systems, decision-making, rationality. [*Behav Ecol*]

In its original economic setting, rational choice theory predicts behavior under the assumption that humans act to maximize utility, an implicit measure of net benefit (von Neumann and Morgenstern 1944). Applied to behavioral ecology, the theory makes an analogous assumption that natural selection has shaped animal decision making to maximize fitness (Stephens and Krebs 1986; Kacelnik 2006). This predicts the evolution of rational animals that rate options according to their fitness benefits and always choose the one with the highest value. The obvious test of this prediction—comparing the fitness outcomes of chosen and rejected options—is generally impractical. Instead, rationality is assessed by looking for adherence to certain consistency principles implied by maximization. For example, a preference for option A over option B should not be altered by addition of a third option, which is less preferred than either A or B. Immunity to such decoys is a hallmark of rationality known as independence from irrelevant alternatives (IIA) (Rieskamp et al. 2006).

Despite these predictions, violations of IIA and other rationality principles have been observed repeatedly in humans and other animals (Tversky 1969; Huber et al. 1982; Wedell 1991; Shafir et al. 2002; Bateson et al. 2003). Irrationality typically arises in challenging decisions involving options with multiple attributes such that no option is clearly superior in all attributes. In the decoy effect, for example, irrational shifts in preference are seen with addition of a decoy option that is clearly inferior to one target option but not to another (i.e., the decoy is asymmetrically dominated) (Huber et al. 1982). The decoy itself is rarely chosen, but its presence typically

increases preference for the dominating target. Such an increase violates the principle of regularity, which holds that an option's popularity should not be increased by the addition of new options to the choice set (Rieskamp et al. 2006).

Rationality violations seem to cast doubt on the optimizing power of natural selection, but an alternative explanation points to the influence of constraints unrecognized by classical rational choice theory. This classical theory assumes that decision makers have unlimited cognitive resources, but real animals operate under strong constraints both in the information they possess and the means to process it (Simon 1982). These constraints may select for simple heuristics or rules of thumb that economize on computation by either excluding information or processing it imperfectly (Gigerenzer and Todd 1999, 2000; Hutchinson and Gigerenzer 2005). In particular, it may be easier for an animal to compare the options in a choice set than it is to estimate the absolute fitness value of each one (Tversky and Simonson 1993; Shafir 1994; Bateson et al. 2003; Bateson and Healy 2005). In the decoy effect, only the dominant target is a clear winner in any pairwise comparison, thus enhancing its attractiveness to individuals using comparative heuristics. Selection may favor these heuristics if they work well in commonly encountered natural settings. However, these same rules may fail in certain predictable contexts, like the experimental paradigms that reliably yield irrational choice (Ariely 2008; Livnat and Pippenger 2008).

If comparative heuristics lie behind irrational choice, then a different pattern may arise in the collective decisions of highly integrated groups, such as insect societies. In these "superorganisms," selection at the group level has yielded sophisticated colony-level adaptations, including the ability to reach consensus on the best of several options. A colony's choice arises in a highly decentralized way without the need for direct comparisons between options by individual ants

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(Couzin et al. 2005; Pratt and Sumpter 2006; Seeley et al. 2006; Hölldobler and Wilson 2008; Gordon 2010). The process is well illustrated by nest-site selection in *Temnothorax* ants, which typically live in preformed natural cavities, such as rock crevices or hollow nuts (Franks et al. 2002; Pratt et al. 2005; Pratt and Sumpter 2006; Robinson et al. 2009). In the laboratory, colonies thrive in artificial cavity nests made of glass and wood or cardboard. When presented with 2 such nests of different design, a homeless colony can assess each on the basis of multiple attributes and emigrate to the better one (Pratt and Pierce 2001; Franks, Mallon, et al. 2003). This decision arises from a complex algorithm based on competition between recruitment efforts by scout ants, few of which assess more than one candidate (Mallon et al. 2001; Pratt et al. 2005; Pratt and Sumpter 2006; Robinson et al. 2009). In a study of 9 emigrations by *T. albipennis*, for example, only 27% of scouts visited both sites in time to influence the colony's decision (Robinson et al. 2009). The majority with knowledge of only one site nonetheless drive the decision process because they start to bring nest mates to their site with a probability that depends on its quality (Mallon et al. 2001; Pratt 2005). As a result, population growth at the better site outstrips its competitor, ultimately making it the colony's choice.

We hypothesized that this highly distributed mechanism may save colonies from the irrational consequences of comparative heuristics. This is because a colony's choice emerges from the behavior of many ants that have each assessed only a single site and thus have no opportunity to make comparisons. Consistent with this idea, an earlier study found that colonies of *T. curvispinosus* choosing among nest sites were immune to the decoy effect (Edwards and Pratt 2009). Likewise, house-hunting colonies of *T. albipennis* were found to show transitive preferences, fulfilling another expectation of rationality (Franks, Mallon, et al. 2003). These studies, however, looked only at the decisions of whole colonies and not those of individual ants. Thus, the colony's immunity did not necessarily reflect the suppression of individual errors. It may instead have been a simple result of the particular set of options presented. For example, the trade-off between targets may have been too weak, allowing a strong preference for one target to mask or eliminate smaller decoy effects.

In this study, we carried out a direct test of the hypothesis that collective decision making can eliminate the irrational errors to which individuals are vulnerable. To do this, we challenged both colonies and isolated individuals of *T. rugatulus* with the decoy effect taking care that the target options were closely balanced in attractiveness to maximize the decision challenge. We predicted that a lone ant required to select a site by herself would be vulnerable to the same irrational outcomes seen in solitary animals. A colony, in contrast, should be rationally consistent because it does not rely on comparisons by individuals.

## MATERIALS AND METHODS

### Nest designs

To test for the decoy effect, we designed 2 target nests A and B that posed a trade-off between entrance size and interior illumination. These attributes are important to *Temnothorax*, with colonies showing a strong preference for smaller entrances and darker interiors (Pratt and Pierce 2001; Franks, Mallon, et al. 2003; Pratt 2005). Nest A had a smaller entrance than nest B (2 vs. 5.5 mm) but a brighter interior (1400 vs. 2 lux). We settled on these particular designs through a series of preference tests with different candidates until we found a pair of targets for which ants showed roughly equal preference. We also designed 2 asymmetrically dominated decoy nests. Decoy

$D_A$  was dominated by A but not by B: It shared A's entrance size, but it had a brighter less preferred interior (1400 lux), and it was not dominated by B because of the latter's larger less preferred entrance size. Decoy  $D_B$ , in contrast, was dominated by B but not by A: It equaled B in illumination but trailed it in entrance size (9.5 mm), and it was not dominated by A because of the latter's brighter less preferred interior. Figure 1 summarizes the dominance relationships between targets and decoys.

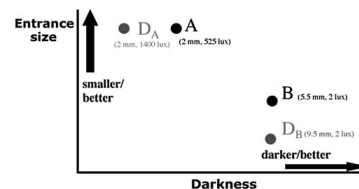
Each nest was made from a balsa wood slat (2.4-mm thick) sandwiched between glass microscope slides ( $50 \times 75$  mm). A circular cavity (38-mm diameter) was cut through the middle of the slat, and a round entrance hole was drilled through the center of the roof. The roof was composed of 2 identical slides stacked on top of one another. Interior illumination was adjusted by placing transparent neutral density filters (Rosco Cinegel) between the roof slides. This design prevented ants from directly contacting the filters, which can sometimes build up an electrostatic charge that the ants find repellent. All filters had a 9.5-mm diameter hole to accommodate the nest entrance. Consistent hole size ensured that illumination was independent of entrance size.

Nests were illuminated by 2 fluorescent light fixtures suspended 37 cm above the bench on which all experiments were carried out. This provided even illumination of 1400 lux at the benchtop as measured by a Lutron LX-101A light meter. Each fixture had a single 8000 °K T-8 full-spectrum daylight bulb (Aqueon Products All-Glass Aquarium, Franklin, WI).

### Subjects

Fifty-three colonies of *T. rugatulus* were used for the colony-level tests. An additional 6 colonies provided 53 worker ants for the individual tests. Only a minority of workers in *Temnothorax* colonies participate actively in nest-site scouting and transport of nest mates and brood items, whereas the rest of the colony waits at the home nest (Mallon et al. 2001; Pratt 2005). In order to ensure that we tested only these active ants, we placed brood items outside of the colony's nest and selected workers that attempted to retrieve them. We reasoned that ants willing to leave the nest and retrieve brood were likely to carry out similar tasks during colony emigration.

Colonies were collected in the Pinal Mountains near Globe, Arizona. All had at least one queen, with worker populations ranging from 120 to 250 and brood populations ranging from 8 to 90. Each colony was housed in a nest like those described above but with a small entrance (2.0-mm diameter) and no light filter. Each nest was kept in a plastic box ( $11 \times 11$  cm), the walls of which were coated with Fluon to prevent the ants



**Figure 1**

Attributes of nests used in preference tests. The choice between target nests A and B imposes a trade-off in 2 attributes: A is better than B in regard to entrance size but B is better than A in regard to darkness. Decoy nests  $D_A$  and  $D_B$  are asymmetrically dominated by the targets:  $D_A$  is clearly worse than A but not B, whereas  $D_B$  is clearly worse than B but not A.



from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (Bhatkar and Whitcomb 1970).

### Individual experiment

We first performed binary preference tests between targets A and B to confirm that the trade-off between entrance size and cavity illumination posed a significant decision-making challenge. If so, we predicted that each nest design would be chosen roughly half the time. The 2 nests were placed adjacent to one another against one wall of a small experimental arena with Fluon-coated walls ( $17.8 \times 12.7$  cm). We placed 3 brood items inside each nest and then introduced a single test subject into the arena. The subject was placed on the arena floor near the center of the wall opposite to the location of the nests. To determine her preference, we took advantage of the tendency of ants to gather scattered brood into a preferred location (Franks and Sendova-Franks 1992). The ant's choice was assayed after 12 h by recording the site to which she had carried all 6 brood items. In this and all other preference tests, the position of the target nests was randomized to control for directional bias.

We then used a similar procedure to determine whether the presence of a decoy site changes preference between A and B. The procedure was modified to ensure that each subject experienced the decoy nest before making her choice. We first placed the decoy nest alone in the arena against one wall. We then deposited 3 brood items just outside the entrance of the decoy and introduced a single test subject to the arena. The arena was checked periodically to see whether the ant had moved the brood inside. All ants did so within 12 h, confirming that they had experienced the decoy. After this, the procedure was identical to the binary choice experiment. Target sites A and B, each containing 3 brood items, were placed near the center of the arena wall opposite from the decoy. Preferences were assayed after 12 h by recording the site that contained all 9 brood items (the 6 in the target nests as well as the 3 from the decoy nest). We used this 2-stage method rather than simultaneous presentation of all 3 options because the latter approach leaves open the possibility that the ant makes a decision without first visiting the decoy, thus undermining the essential condition for testing the decoy effect.

Twenty ants were given the binary choice between A and B; 16 were tested with decoy  $D_A$ , and 17 with decoy  $D_B$ . Each ant was tested only once. No ant ever chose the decoy. Nine ants did not choose a nest (2 in the binary test, 2 in the presence of decoy  $D_A$ , and 5 in the presence of decoy  $D_B$ ) and so were excluded from the analysis.

### Colony experiment

To confirm that colonies showed similar preferences to those of individuals, we performed binary preference tests between targets A and B. The procedure was identical to that for individuals except that all members of the colony, rather than a single ant, were removed from their home nest and deposited in a test arena containing the target sites.

Then, to test the effect of decoys on whole colonies, we used a similar procedure to that for individual ants. First, a colony was introduced to the experimental arena in its home nest, and an empty decoy nest (either  $D_A$  or  $D_B$ ) was placed nearby. The colony was then induced to migrate to the decoy by removing the roof of its home nest. All colonies successfully migrated within 12 h. Target nests A and B were then placed against the arena wall opposite from the decoy. In contrast to the individual experiment, the roof of the decoy was removed to induce

migration. We assayed nest-site preference by recording the site occupied by the colony 12 h later. Colonies usually showed an unambiguous preference, but they sometimes split between sites. If one site contained more than 90% of colony members, including all queens and brood items, we designated that as the colony's choice. If no site achieved this criterion, we did not record a preference. This occurred only 8 times out of 60 migrations. Thirty colonies were tested, each one receiving both the  $D_A$  and the  $D_B$  treatments in counter-balanced order.

### Preparation

Before each experiment, all glass slides were washed with dish soap and rinsed with distilled water. Light filters were gently wiped with ethanol, and the experimental arena was cleaned with ethanol. Balsa slats were made fresh for each experiment and never reused.

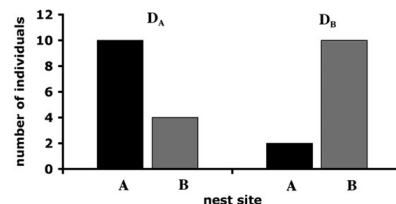
### Analysis

Preferences in the binary choice were assayed with a binomial test. The presence of a decoy effect was tested with a  $\chi^2$  test of independence. That is, we tested the null hypothesis that the preference between targets A and B was independent of the type of decoy present. The alternative hypothesis was that the 2 decoy types drive target preference in opposite directions with  $D_A$  making A more popular and  $D_B$  making B more popular. The statistical package R (v. 2.9.0) was used for all analyses, and Yate's continuity correction was applied in all  $\chi^2$  tests.

## RESULTS

### Individual ants show irrational preference shifts

In the binary choice between A and B, individual ants showed no strong preference for either site, with 9 choosing A and 9 choosing B (2-tailed binomial test:  $P = 1.0$ ). This result confirmed that the trade-off between entrance size and dimness posed the desired decision-making challenge to individuals. In the presence of an asymmetrically dominated decoy, however, the preference between A and B was significantly altered. Target A was preferred to B in the presence of  $D_A$ , but B was preferred to A in the presence of  $D_B$  ( $\chi^2 = 7.79$ , degrees of freedom [df] = 1,  $N = 26$ ,  $P < 0.05$ ) (Figure 2). Thus, the addition of a decoy option to the choice set caused individuals to violate regularity by increasing their preference for the dominant target.



**Figure 2**  
Nest-site preference by individual ants depended on which decoy nest was present. In the presence of  $D_A$ , more ants chose A, whereas in the presence of  $D_B$ , more ants chose B ( $\chi^2 = 7.79$ ,  $N = 26$ ,  $P < 0.05$ ).

### Colonies show rationally consistent preferences

Like individuals, colonies showed no strong preference in the binary choice, with 11 choosing A and 12 choosing B (2-tailed binomial test:  $P = 1.0$ ). In contrast to individuals, however, colony preferences were unaffected by asymmetrically dominated decoys ( $\chi^2 = 0.734$ ,  $df = 1$ ,  $N = 52$ ,  $P = 0.392$ ) (Figure 3). Preferences were not identical between the 2 treatments, but the difference was nonsignificant and opposite to the direction predicted by the decoy effect and observed in the individual experiment. This result cannot be attributed to low sample size as power analysis showed that this sample size is adequate to detect an effect as strong or stronger than that seen in the individual experiment (power = 0.98 for  $\alpha = 0.05$ ).

To exclude the possibility that removal of the decoy roof was responsible for the difference between individuals and colonies, we repeated the  $D_B$  treatment but allowed colonies to spontaneously abandon the undamaged decoy (colonies were unwilling to abandon undamaged  $D_A$  nests). If the decoy influences preferences in the same way seen for individuals, we expected to see a preference for B over A in these tests. Instead, we again saw only a nonsignificant trend in the opposite direction (9 chose A and 6 chose B; 2-tailed binomial test,  $P = 0.607$ ).

### DISCUSSION

The consistency of colony preferences in these experiments confirms an earlier result from *T. curvispinosus* (Edwards and Pratt 2009). That study examined only colony-level behavior, but the new results show clearly that lone ants are strongly influenced by decoys that have no effect on colonies. Similar sensitivity has been shown for individuals of many other species, but the decoy effect observed here was especially strong. For example, some earlier studies found no violation of regularity but only of the weaker constant ratio rule, which holds that the relative popularity of 2 options should not be changed by adding a third option (Bateson et al. 2002). Other studies found regularity violations but in response to only 1 of the 2 decoys offered (Bateson et al. 2003). The stronger effect in our study may be due to our careful selection of equally preferred targets posing a challenging trade-off between attributes. More importantly, it shows that the rational consistency of colony behavior was not simply a function of our choice set—instead, colonies showed clearly rational behavior in a context that induced strong departures from rationality in lone ants.

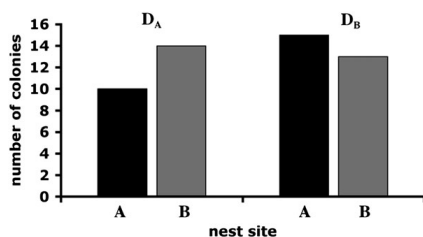
This contrast between group and individual reverses a traditional view that collectives are prone to amplification of individual irrationality. Our results instead suggest that an appropriately structured collective can prevent irrationality by avoiding the

overburdening of individual cognitive abilities. A plausible scenario is that lone ants cannot adequately process information for all 3 nests when inconsistencies among their attributes complicate assessment. Instead, ants may rely on simplifying heuristics based on pairwise comparisons, which are also implicated in the decoy effects seen in humans and other animals (Hastie and Dawes 2001; Bateson and Healy 2005). In a collective setting, such comparisons are unnecessary because each ant need assess only one site or at most compare it to her current home. This limited perspective imposes the best strategy for consistent choice: evaluate a given option the same way regardless of the available alternatives. The separate evaluations of many ants are then integrated through a communication network and complex behavioral algorithm (Pratt et al. 2005; Pratt and Sumpter 2006). The result is emergence of a rational group decision from ants prone to individual irrationality.

Under this scenario, the group paradoxically benefits by limiting the information available to each of its members. In laboratory emigrations by *Temnothorax* colonies, such limited information is the rule: Most ants do not visit more than one of the available candidate sites or do so only after decision making is well underway (Mallon et al. 2001; Robinson et al. 2009). This is not necessarily an adaptive response by the colony but a constraint imposed by the great difference in scale between ants and the area they must search. It is unlikely for each ant to find more than one site in time to influence the colony. Some ants, however, do get to visit more than one site. What impact might they have on the colony's choice? Robinson et al. (2009) suggest that even these knowledgeable ants refrain from making comparisons partly to avoid the resulting risks of irrational inconsistency. Our results, however, contradict this idea. If informed individuals do not compare options, then we should not have seen any influence of the decoy on the preferences of isolated ants. Instead, decoys strongly changed individual preferences between A and B. In a colony setting, however, this effect may have relatively little influence on the collective decision. Even if some ants show irrational behavior, their influence is likely swamped by the much larger number of ants that do not have the opportunity to compare sites.

Although a long line of research has noted the error-reducing potential of collective choice, the focus has been on random errors that can be cancelled out by a straightforward process of summation (Grunbaum 1998; Conradt and Roper 2003; Franks, Dornhaus, et al. 2003; Simons 2004; Surowiecki 2004; Ward et al. 2008). For example, a group of migrants may average their noisy estimates of the proper travel direction to achieve a more precise heading. In contrast, the decoy effect and other cases of irrational choice involve systematic preference changes that cannot be cancelled out by summing the choices of many independent decision makers (Livnat and Pippenger 2008). Collective choice can only limit these errors if it allows individuals to show qualitatively different behavior in the social context than they do when alone. For the ants, the key difference is that lone ants must make comparisons, but ants in the social context need not. Comparison of options is instead an emergent property of the colony as a whole.

This reasoning suggests that differences in the structure of individual and group cognition explain the contrast we observed. However, we must also consider whether the explanation lies in other differences between the 2 cases. An obvious methodological difference is that lone ants spontaneously abandoned the intact decoy nest to choose one of the targets, whereas colonies left the decoy only after its roof was removed. Destruction of their nest might spare colonies from the decoy effect if ants rapidly forget the attributes of their ruined home. This possibility is discounted by the behavior of colonies that



**Figure 3**  
Nest-site preference by colonies was not affected by decoy type ( $\chi^2 = 0.734$ ,  $N = 52$ ,  $P = 0.392$ ).

were allowed to abandon an intact nest just like the lone ants. Colonies did this only when living in decoy  $D_b$ , but their preferences were indistinguishable from those of colonies forced from  $D_b$  by removal of its roof. That is, they showed no preference for the dominant target just as expected under rational choice. This is consistent with earlier work that found an effect of home nest quality on emigration behavior even after the home was destroyed (Healey and Pratt 2008).

Another possible confounding factor is the unnatural isolation of ants in the individual experiments. This may have caused very different motivational states or preference functions than the same ants would show in a colony context. For example, isolated ants might hastily seek any haven for their brood rather than deliberating over the best nest. This possibility is countered by the slow decision speeds of these ants; rather than rush into any shelter, they spent at least as long as whole colonies before moving the brood to their final choice. The first check of experimental arenas was typically made 3 to 5 h after introducing the target nests; although most colonies had made a decision by this point, few individuals had. More importantly, lone ants and colonies showed very similar preferences in the binary choice when only the target sites A and B were present, suggesting that the lack of social context did not strongly alter preferences. Even if isolation did influence choice behavior, this would not change the essential irrationality of the lone ants' behavior compared with that of colonies. Whatever a decision-maker's preferences, they should remain consistent in the presence of an unattractive decoy. Lone ants strongly violated this expectation, whereas colonies did not.

These findings emphasize the importance of context in evaluating decision-making behavior. Like other ants, *Temnothorax* are obligately social, typically making nest-site choices collectively rather than relying on fully informed individuals. In this sense, the ants are ecologically rational (Stephens et al. 2004)—their behavior maximizes fitness in natural settings, if not in the experimental context of isolated ants. The finding that rationality is attained by the group, despite the potential for irrationality by individual members, suggests a novel advantage to group living and one that may also prove relevant to other social animals.

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## APPENDIX C

### GROUPS HAVE A LARGER COGNITIVE CAPACITY THAN INDIVIDUALS

images, demonstrating that the effect is not driven by incidental stimulus-related characteristics. Further, threatening — but not non-threatening — stimuli were judged as arriving earlier than scrambled versions of the same images, suggesting that the effect is driven specifically by responses to threatening stimuli.

Experiment 3 investigated whether reduced time-to-collision judgments could reflect a non-specific effect of seeing threatening stimuli, such as heightened arousal. Participants saw threatening or non-threatening stimuli for one second, immediately followed by a looming blue disc. If the effect we report is a non-specific effect of seeing threatening stimuli, time-to-collision judgments of the blue disc should be faster when preceded by images of threatening stimuli. Contrary to this prediction, priming images had no apparent effect on time-to-collision judgments of a semantically-neutral disc.

Threatening stimuli are perceived as approaching more rapidly than non-threatening stimuli, especially for those who are fearful of those objects. These results show, in contrast to the traditional view of looming as a purely optical cue to object approach [1], that perceiving the time of imminent collision is not entirely driven by purely optical cues, but is also subject to emotional modulation. Gibson and colleagues [1] pointed out that as an optical cue to imminent collision, visual looming is a direct perceptual indicator of threat. Our results suggest that the affective content of looming stimuli also affects perceived time-to-collision. Underestimating arrival time of threatening stimuli may thus serve an adaptive role in leading responses to err on the side of additional time for either fight or flight. Some perceptual biases appear only for explicit perceptual judgments, but not for visually-guided actions [5]. Thus, it is possible that the present effect reflects a purely perceptual distortion that might not affect actions, such as catching.

Recent findings have demonstrated that emotion modulates some basic aspects of perception, such as visual contrast sensitivity [6], but not others, such as auditory directional attention [7]. The selectivity of emotional effects on perception is consistent

with anecdotal reports that specific phobias may induce category-specific distortions of perception [8]. Though we investigated variability in fear in an unselected sample (i.e. generally non-phobic), our results provide experimental evidence consistent with this proposal. Other recent results have also suggested that individual differences in fear, even in the non-clinical range, alter space perception. For example, fear of heights is associated with distorted perception of vertical distance [9], whereas claustrophobic fear is associated with increased size of the near space immediately surrounding the body [10]. The present results fit with and extend these by showing that emotion not only alters the perception of space as a static entity, but it also affects the perception of dynamically moving objects, such as those on a collision course with the observer.

#### Supplemental Information

Supplemental Information includes experimental procedures and two figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.07.053>.

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## Groups have a larger cognitive capacity than individuals

Takao Sasaki and Stephen C. Pratt

Increasing the number of options can paradoxically lead to worse decisions, a phenomenon known as cognitive overload [1]. This happens when an individual decision-maker attempts to digest information exceeding its processing capacity. Highly integrated groups, such as social insect colonies, make consensus decisions that combine the efforts of many members, suggesting that these groups can overcome individual limitations [2–4]. Here we report that an ant colony choosing a new nest site is less vulnerable to cognitive overload than an isolated ant making this decision on her own. We traced this improvement to differences in individual behavior. In whole colonies, each ant assesses only a small subset of available sites, and the colony combines their efforts to thoroughly explore all options. An isolated ant, on the other hand, must personally assess a larger number of sites to approach the same level of option coverage. By sharing the burden of assessment, the colony avoids overtaxing the abilities of its members.

Nest site selection by *Temnothorax* ants exemplifies collective decision-making without well-informed leaders [5]. When a colony must find a new home, it can choose the better of two new sites even when no single ant assesses both. Instead, comparison emerges from a competition between recruitment efforts. Upon finding a site, an ant recruits nestmates to it with a probability that depends on the site's quality, as determined by entrance diameter, cavity size, light level, and other features [6]. Her recruits make their own quality-dependent recruitment decisions, creating positive feedback that directs the colony towards the better nest. Consensus is further enhanced by a quorum rule that accelerates recruitment once a site's population has surpassed a threshold [5].

Although this process does not require individuals to compare sites, they have the ability to do so; an isolated ant that assesses two sites of different quality can reliably choose the better one [7]. We took advantage of this fact to compare the cognitive capacity of groups and individuals. We induced subjects (either whole colonies or isolated ants of *T. rugatulus*) to select a new nest in one of two conditions. In the simpler condition they chose between only two nests, one good and one poor. In the more challenging condition, they chose among eight options, four good and four poor (Figure 1A). Good nests differed only in having a smaller entrance, a strongly favored feature [6]. Decision performance was measured by noting which type of nest the subject moved into.

We found that individuals performed significantly worse when the number of options was eight rather than two, indicating that they experienced cognitive overload ( $\chi^2 = 4.18$ ,  $N = 43$ ,  $df = 1$ ,  $p < 0.05$ ). In the two-nest condition, over 80%

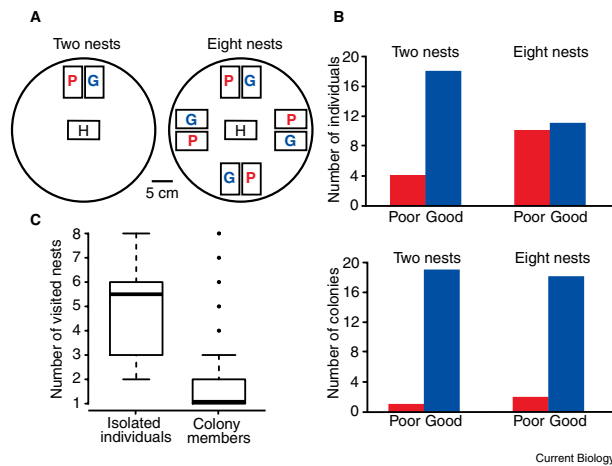
of ants chose a good nest, but in the eight-nest condition, only 50% did, indistinguishable from random performance. Colonies, on the other hand, performed equally well with either two or eight options, with at least 90% choosing a good nest in each condition ( $\chi^2 = 0.36$ ,  $N = 40$ ,  $df = 1$ ,  $p = 0.55$ ) (Figure 1B). Thus, colonies achieved a significantly higher decision performance in the face of increased processing load than did individuals (partial  $\chi^2$  test:  $\chi^2 = 8.75$ ,  $N = 3$ ,  $df = 3$ ,  $p = 0.03$ ).

We hypothesized that colonies better handle higher option numbers because their members do not have to assess as many sites as isolated individuals. If so, we predicted that each colony member visits a smaller number of nests than an isolated ant. To test this, we repeated the eight-nest treatment, but counted the number of sites visited by each ant. The results of this second experiment confirmed our prediction: isolated ants assessed significantly more sites than did colony members (Wilcoxon rank test:  $W = 1819$ ,  $N_{\text{isolated}} = 10$ ,  $N_{\text{colony}} = 209$ ,

$p < 0.01$ ) (Figure 1C). Importantly, although each colony member visited very few sites, the colony collectively assessed all eight sites.

The inferior performance of isolated ants cannot be explained as a simple artifact of isolating these normally very social animals. Lone ants performed just as well as colonies when choosing between two sites; only with an increase in option number did their ability to select a good nest decline (Figure 1B). Nor can the colony advantage be ascribed to a higher probability of finding a good site. Because half of the options were good in both conditions, the probability of finding a good nest did not depend on the number of options available for either colonies or individuals (see the Supplemental Information for details). Furthermore, when isolated ants were tracked in the second experiment, all of them found at least one good nest. Indeed, they found many more sites than did all but a few individual colony members (Figure 1C). The small minority of colony members that visited a large number of nests contributed little to total transport effort, and thus to the colony's decision (see the Supplemental Information for details). Therefore, we attribute the worse performance of isolated ants to the difficulty of processing a greater load of data. We cannot say why isolated ants do not avoid this problem by simply assessing fewer sites. However, we speculate that they prolong their search for new nests because they lack social interactions, such as quorum attainment, that would normally trigger earlier acceptance of a site.

Cognitive overload is a growing issue for human decision-making, as unprecedented access to data poses new challenges to individual processing abilities [1]. Human groups also solve difficult problems better when each group member has only limited access to information [8]. For social insects, this advantage is likely much greater, because natural selection on colony-level phenotypes has shaped particularly elaborate and highly integrated group cognition. This is because selection acts largely through the reproductive success of whole colonies, rather than that of the sterile workers that make them up [9].



**Figure 1. Effect of option number on decision performance.** (A) Experimental arenas. Subjects (whole colonies or isolated ants) were made to abandon their home nest (H) and choose a new nest from an array of either two or eight good (G) and poor (P) options. (B) Numbers of subjects choosing good or poor nests in each treatment. Isolated ants made worse decisions with eight options than with two (top chart), but colonies nearly always chose a good nest regardless of the number of options (bottom chart). (C) In the eight-nest condition, isolated ants visited more nests than did individual colony members. Boxes delimit the 1<sup>st</sup> and 3<sup>rd</sup> quartiles, the horizontal line indicates the median, and whiskers show the range. Open circles are outliers.



It has long been recognized that collective choice can improve accuracy by averaging out the random errors of inaccurate individual decisions [3]. The advantage we find here is different: rather than combining many essentially identical choices, colonies truly distribute their decision-making. No worker must carry out the full task of assessing and comparing all options, allowing the colony as a whole to process more information, more effectively. This advantage can serve as a model for the rapidly developing field of collective robotics, which looks to the robust, decentralized group behavior of social animals for biologically inspired design ideas [10].

#### Supplemental Information

Supplemental Information includes experimental procedures, results and two figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2012.07.058>.

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## Opponency of astringent and fat sensations

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In most cultures, people ingest a variety of astringent foods and beverages during meals, but the reasons for this practice are unclear. Many popular beliefs and heuristics, such as high tannin wines should be balanced with fatty foods, for example ‘red wine with red meat’, suggest that astringents such as pickles, sorbets, wines, and teas ‘cleanse’ the palate while eating. Oral astringents elicit ‘dry, rough’ sensations [1], in part, by breaking down mucinous lubricating proteins in saliva [2,3]. The introduction of oral lubricants, including fats, partially diminishes strong astringent sensations [4,5]. Thus, it appears that astringency and fattiness can oppose each other perceptually on an oral rheological spectrum. Most teas, wines, and ‘palate cleansers’, however, are only mildly astringent and an explanation of how they could oppose the fattiness of meals is lacking. Here, we demonstrate that weakly astringent stimuli can elicit strong sensations after repeated sampling. Astringency builds with exposures [6] to an asymptotic level determined by the structure and concentration of the compound. We also establish that multiple sips of a mild astringent solution, similar to a wine or tea, decrease oral fat sensations elicited by fatty food consumption when astringent and fatty stimuli alternate, mimicking the patterning that occurs during a real meal. Consequently, we reveal a principle underlying the international practice of ‘palate cleansing’. Repeatedly alternating samples of astringent beverages with fatty foods yielded ratings of fattiness and astringency that were lower than if rinsing with water or if presented alone without alternation.

Three astringents — grape seed extract (GSE), epigallocatechin-gallate (EGCG) from green tea, and

aluminum sulfate (Alum) — were evaluated by volunteers for perceived astringency intensity over the course of 80 oral exposures (sips). The astringency intensity curves grew exponentially over exposures, regardless of the compound or concentration (Figure 1A and Figure S1 in the Supplemental Information). Each astringent solution, however, elicited distinct maxima (a + y0) depending on the concentration level. Weakly concentrated solutions never reached the astringency maxima of more concentrated solutions of the same compound. In addition, the rate (b) at which maximal intensity was reached over trials varied with both the chemical structure and concentration (Figure 1B). Here, Alum and EGCG solutions reach their astringency maxima faster at high concentrations than low, whereas GSE solutions reach their maximum at the same rate regardless of the concentration.

After establishing that weak astringents could elicit strong astringency with repeated sampling, we asked subjects to rate fattiness and astringency, after ingesting pieces of fatty food (dried meat) alternating with multiple sips of one of two rinsing solutions (tea or water). Astringent rinses affected oral sensations. In particular, the perceived fattiness was less pronounced after drinking tea than after drinking water (Figure 1C left panel). Thus, astringent consumption during meals provided a greater reduction of oral fattiness compared to water rinses. We also observed a more significant growth of astringency sensation with multiple sips without eating a fatty food, indicating that fat reduced the build-up of astringency (Figure 1C right panel). Similarly, there was a greater increase of fatty sensation from repeated fatty food consumption without any rinsing (Figure 1D left panel). These observations support the hypothesis that these sensations oppose each other perceptually and lie at different ends of an oral rheological/tribological sensory spectrum.

The oral perceptions of fattiness and astringency largely depend on tactile sensations [7]. Frictional rubbing of the oral epithelia is very important for food tactile perception. For example, foods are commonly assessed mechanically *ex vivo* using a tribometer, which measures the



## Supplemental materials

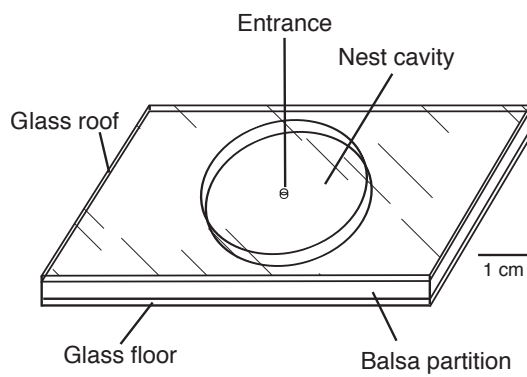


Figure S1. Nest design.

Nests were constructed from a balsa wood slat with a circular hole drilled through its center. The roof and floor of the nest were made of glass microscope slides.

An entrance hole was drilled through the center of the roof.

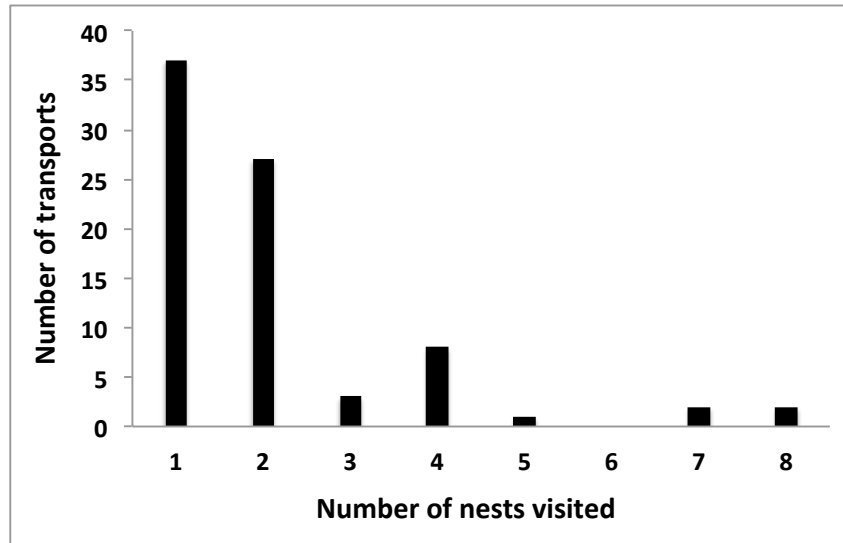


Figure S2. Number of brood items transported as a function of the number of nests visited. Each bar shows the total number of brood transports by all ants that visited a given number of nests during a colony emigration.

## S1. Materials and Methods

### *Nest designs*

Each nest was made from a balsa wood slat (2.4 mm thick) sandwiched between glass microscope slides (50 x 75 mm). A circular cavity (38 mm diameter) was cut through the middle of the slat, and a round entrance hole was drilled through the center of the glass roof (Figure S1). To test for the existence of cognitive overload, I designed two kinds of target nests, good and poor. These nests were identical except for their entrance sizes: The good nest had a smaller entrance ( $\varnothing = 2$  mm) than did the poor nest ( $\varnothing = 5.5$  mm). Small entrances are known to be of importance to *Temnothorax* ants, presumably because they are more defensible and allow better control of the interior nest environment (Franks et al., 2003; Visscher, 2007). Subjects started each experimental trial in a standard home nest with an intermediate entrance size ( $\varnothing = 3.2$  mm).

### Subjects

45 colonies of *Temnothorax rugatulus* were used for the colony-level tests. An additional 13 colonies provided 52 worker ants (four ants per colony) for the individual tests. Only a minority of workers in *Temnothorax* colonies participate actively in nest-site scouting and transport of nestmates and brood items, while the rest of the colony waits at the home nest (Mallon et al., 2001; Pratt, 2005). In order to ensure that I tested only these active ants, I placed brood items outside of the colony's nest and selected workers that attempted to retrieve them. I

reasoned that ants willing to leave the nest and retrieve brood were likely to carry out similar tasks during colony emigrations (Sasaki & Pratt, 2011).

Colonies were collected in the Pinal Mountains near Globe, Arizona (N 33° 19.00', N 110° 52.56', W). All had at least one queen, with worker populations ranging from 100 to 250 and brood populations ranging from 80 to 300. I estimate that 25 to 100 ants (one third of each colony's worker population) actively participated in scouting, site assessment, and recruitment. Each colony was housed in a nest like those described above, but with a small entrance ( $\varnothing$  = 2 mm). Each nest was kept in a plastic box (11 cm x 11 cm), the walls of which were coated with Fluon to prevent the ants from escaping. Each box was provided with a water-filled plastic tube capped with cotton and an agar-based diet that was refreshed weekly (Bhatkar & Whitcomb, 1970).

*Experiment 1: Do colonies have larger cognitive capacities than individuals?*

I compared the decision performance of individuals and colonies when offered either two or eight nest sites. For individuals, a home nest with two brood items was placed in the center of a circular arena (34 cm diameter and 3 cm wall). To ensure that each individual was aware of the home nest and the brood items, I deposited the brood just outside the entrance of the home nest and introduced a single individual to the arena. The ant was given 12 hours to find the nest and move the brood inside. Then, I placed either 2 target nests (1 good and 1 poor) or 8 target nests (4 good and 4 poor) in the arena. In the 8-nest condition, a pair of nests (one good and one poor) was placed at each of four equally spaced locations around the centrally located home nest (north, south, east, and west).

The same nest configuration was used for all trials (Figure 1A). In the 2-nest condition, a pair of nests was placed in only one of the four locations, randomly chosen for each trial. The distance from the home nest to each of the target nests was 10 cm. To induce a move to one of the target nests, the roof of the home nest was removed. The ant's choice was assayed after 12 hours by recording the nest to which she had carried the brood items. A total of fifty-two individuals were tested. Six never moved the brood items to the home nest, so I did not test them further. Three of the remaining individuals did not move to a target nest (1 in the two-nest condition and 2 in the eight-nest condition), and so were excluded from the analysis.

For colonies, the procedure was identical to that for individuals except that all members of the colony were used. The colony in its old nest was placed next to a standard home nest in the center of the arena. The roof of the old nest was then removed to induce the colony to move into the home nest. In all cases, colonies finished migrating within 12 hours. Then, target nests were introduced, and the roof of the home nest was removed to induce the colony to migrate. The colony's choice was assayed by recording the nest to which a strong majority of colony members (> 90%) migrated. Among 45 colonies tested, 5 did not choose a target nest (2 in the two-nest condition and 3 in the eight-nest condition), and so were excluded from the analysis.

#### *Experiment 2: Do isolated ants assess more nests than ants within colonies?*

If colonies are less vulnerable to cognitive overload because they distribute the burden of assessing nests, then each colony member should visit a smaller

number of nests than do isolated ants. I carried out a second experiment to test this hypothesis. The experiment was identical to the eight-nest condition: both colonies and isolated ants were again presented with eight target nests and monitored until they moved to one of the nests. However, I counted the number of nests visited by each isolated ant and by each ant within a colony. To allow individual tracking, ants in each colony were painted with distinctive color patterns. Experiments were recorded with a high-resolution camera (Canon t2i) that photographed the entire arena at 5-second intervals. I then examined the photographs to determine the identity of all visitors to every nest. To accelerate this procedure, I used the “batch process” feature of Photoshop to crop and zoom in on each nest in each photograph. Because data were collected at 5-second intervals, I may have missed some very brief visits and thus underestimated the number of nests visited. However, ants usually stay longer than 5 seconds in a nest, especially during their first visit (Mugford et al., 2001). Even if some visits were missed, this should have occurred equally in the two-nest and eight-nest conditions, and so should not bias comparisons between them. I tested 2 colonies and 10 individual ants taken from an additional 5 colonies (two ants per colony). In the colony tests, a total of 198 individual ants were analyzed.

### *Preparation*

The wall of the experimental arena was coated with Fluon to prevent ants escaping. Before each experiment, all glass slides were washed in a commercial

dishwasher, and the experimental arena was cleaned with ethanol. Balsa slats were made fresh for each experiment and never re-used.

### *Analysis*

I separately tested individuals and colonies for cognitive overload using a  $\chi^2$  test of independence. Our null hypothesis was that the number of subjects choosing the good vs. poor nest was independent of condition (two nests vs. eight nests). The alternative hypothesis was that a higher proportion of subjects would choose the poor nest in the eight-nest condition compared to the two-nest condition. To compare the performance of colonies and individuals, I used the three-way (2 x 2 x 2)  $\chi^2$  test of partial independence. This tested the null hypothesis that colonies and individuals showed the same relation between decision performance (proportion choosing a good nest) and condition (two options vs. eight options). The statistical package R (v. 2.9.0) was used for all analyses.

## **S2. Results: contribution to colony migration**

The results of Experiment 2 showed that most colony members visited only a few nests, but a small minority visited many nests (Figure 1C). If this minority significantly contributed to colony decisions, this would contradict the conclusion that colonies avoid cognitive overload by minimizing individual cognitive burdens. To test this, I further analyzed the Experiment 2 data by estimating each ant's contribution to the colony's decision. I did this by counting the number of brood items transported by each ant. I did not include transports of adults, because the position in which an adult is carried obscures the paint marks on the transporter's back. Earlier observations indicate that individual transporters do not discriminate between adults and brood items, so the latter should give an unbiased estimate of the distribution of transport activity across ants. The results show that the vast majority of transport effort was made by ants that visited only one or two nests (Figure S2). The minority that visited many nests, and thus potentially experienced cognitive overload, contributed little to total transport effort, and thus to the colony's decision. This result is consistent with the conclusion that colonies avoid cognitive overload by distributing the burden of assessment across many ants.



### **S3. Results: distribution of assessed nests**

Although half of available nests were good in both the two- and the eight-nest conditions (Figure 1A), subjects may have had a bias for visiting a certain kind of nest. For example, because a poor nest has a larger entrance size than a good nest, it might be easier to discover. Any such bias could modify decision performance because the distribution of visited nests would deviate from that of available nests. To test for a discovery bias, I calculated the proportion of good nests among all discovered nests (i.e. number of visited good nests/number of visited nests). For isolated individuals in the eight-nest condition, this proportion varied (0.33-0.66) but was 0.516 on average. Every colony, on the other hand, found all eight available nests, meaning that the proportion was always 0.5. The same was true for the two-nest condition, where every subject (both colonies and individuals) always found both options. These results show that isolated individuals and colonies did not have a bias for discovering either nest type. Thus I conclude that the low performance for isolated individuals in the eight-nest condition can best be explained by cognitive overload.

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## APPENDIX D

### PERMISSION TO USE PUBLISHED ARTICLES

All co-authors have granted permission to use these articles in this dissertation.